Distribution and Taxonomy of Fishes in the Mackenzie Drainage of British Columbia[1]

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ABSTRACT

New and previously published records are listed for 28 species of freshwater fishes in tributaries of the Mackenzie River in northern British Columbia. Distribution patterns are discussed for all species reaching the continental divide at the Peace River headwaters; some are restricted to one or other side, but 17 species are common to the Peace and Fraser Rivers, suggesting that mountain ranges have served as a check but not an insurmountable obstacle to postglacial expansion. Five species indigenous to the Pacific slope—*Catostomus macrocheilus*, *Richardsonius balteatus*, *Ptychocheilus oregonense*, *Mylocheilus caurinum*, and *Cottus asper*—have evidently penetrated to the Peace River in comparatively recent times. Three species—the flathead chub *Platygobio gracilis*, the trout-perch *Percopsis omiscomaycus*, and the spoonhead sculpin *Cottus ricei*—have not previously been recorded from the province. Evidence is presented that subspecific distinctions are invalid in *Couesius plumbeus* (Agassiz) and *Lota lota* (Linnaeus). *Coregonus coulteri* and *Hybognathus hankinsoni* are reported for the first time from the Mackenzie drainage.

INTRODUCTION

Almost one third of British Columbia lies within the watershed of the Mackenzie River. Three tributaries, the Peace, Liard and Hay Rivers, together drain some 108,000 square miles of the province. This area abuts to the west and south upon the headwaters of the Fraser, Skeena and Stikine Rivers, with in some places only a low height of land separating the Arctic and Pacific drainages. After the latest glaciation the route of repopulation of British Columbia by some species of fish evidently followed these low points in the continental divide. Certain fishes entered the province from the Mackenzie drainage, crossed into the upper Fraser and spread south. Others which originally entered the province from the south have moved north from the Fraser or Skeena watersheds into the Peace River. Some species have reached the height of land from one or other side but have not yet crossed over.

An understanding of the extent to which freshwater fishes have used this route in breaching the continental divide depends on adequate collections from the adjoining watersheds. The fish faunas of the Skeena and Fraser systems have been fairly well sampled, but collections in the Mackenzie drainage of British Columbia have so far been scant.

Recent road construction has opened up what was formerly an inaccessible region. The John Hart highway from Prince George northeast to Dawson Creek,

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and the Alaska highway from there northwest to the Yukon border, together provide an 880-mile traverse of the Peace and Liard drainages in British Columbia. In 1953 Dr. P. A. Larkin and the author collected fishes from 22 localities along this route. That this modest expedition yielded three species of fish previously unrecorded from the province indicates the dearth of former collecting in the region.

Of the area under consideration (Fig. 1, 2B) the southern portion is drained by the Peace River which flows eastward to Lake Athabaska. This lake also receives water from a portion of British Columbia via the Hay River. Lake Athabaska drains north into Great Slave Lake; the latter empties into the Mackenzie River, which flows northward some 800 miles into the Arctic Ocean.

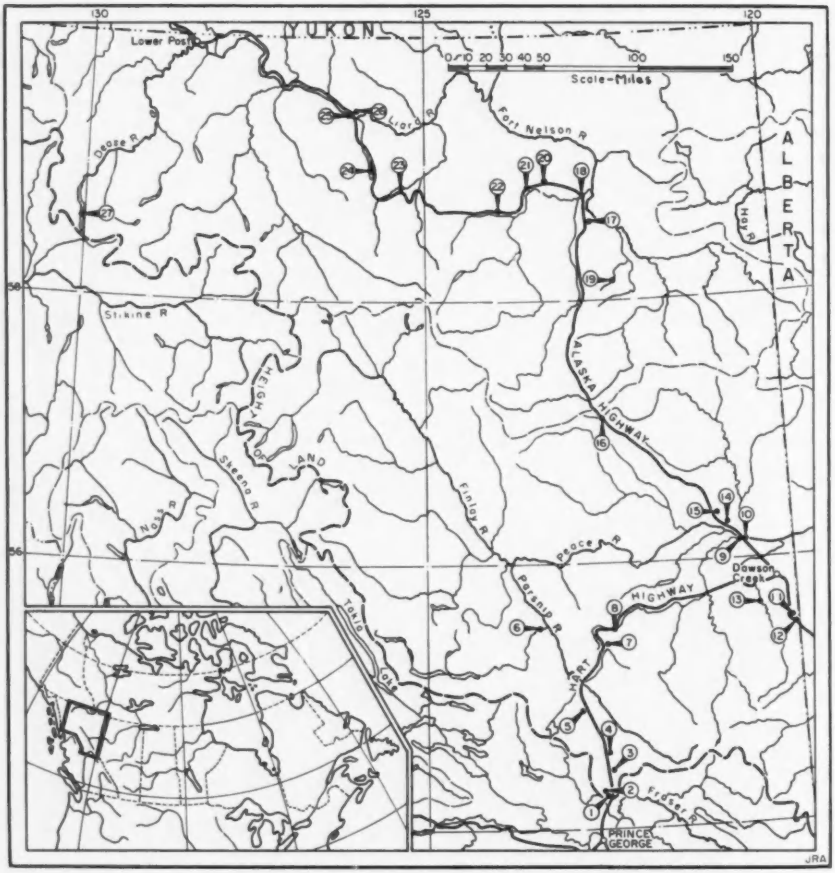

FIG. 1.—British Columbia portion of the Mackenzie River drainage basin. Circled numbers indicate collection sites referred to in Appendix. Watershed boundaries marked by broken lines.

Principal tributaries of the Peace in British Columbia are the Finlay and Parsnip Rivers which lie along the Rocky Mountain Trench.

The other major drainage system in northeastern British Columbia is the Liard River, which enters the Mackenzie in the Northwest Territories some 170 miles downstream from Great Slave Lake. The Liard receives from the south the Dease, Kechika and Fort Nelson Rivers.

A small segment of the Yukon River drainage, which flows 1800 miles to the Bering Sea, rises in northwestern British Columbia and touches on the Liard drainage. On the Pacific slope, headwaters of the Stikine River adjoin both the Liard and Peace headwaters. The remainder of the continental divide touching the Peace drainage separates it from the Skeena and Fraser River drainages. Much of the drainage area considered lies within the mountainous terrain of the Canadian Cordillera, but the eastern portions of both Peace and Liard systems in British Columbia occupy the Interior Plains with gentler profiles and some extensive marshy areas.

Original material and previously published records are summarized in the following paper. Principal sources of published records have been Dymond (1936), Cowan (1939), and Carl and Clemens (1953). Species in the Yukon drainage of British Columbia are listed by Clemens, Boughton and Rattenbury (1945), and in Alaska by Wilimovsky (1954). Ranges outside the province have been compiled largely from Wynne-Edwards (1952), Schultz and DeLacy (1935), Dymond (1947) and Hubbs and Lagler (1947).

The following changes from nomenclature in Carl and Clemens (1953) are made in conformity with recent International Rules of Zoological Nomenclature, or with now generally accepted lumping of closely allied genera (Bailey, 1951a; Eschmeyer and Bailey, 1955) or for reasons stated in the text.

Prosopium coulteri (Eigenmann and Eigenmann) becomes *Coregonus coulteri* Eigenmann and Eigenmann.
Prosopium williamsoni (Girard) becomes *Coregonus williamsoni* Girard.
Prosopium cylindraceum quadrilaterale (Richardson) becomes *Coregonus cylindraceus* Pallas.
Leucichthys sardinella (Valenciennes) becomes *Coregonus sardinella* Valenciennes.
Stenodus leucichthys mackenziei (Richardson) becomes *Stenodus leucichthys nelma* (Pallas).
Thymallus signifer (Richardson) becomes *Thymallus arcticus signifer* (Richardson).
Cristivomer namaycush (Walbaum) becomes *Salvelinus namaycush* (Walbaum).
Catostomus commersonni (Lacépède) becomes *Catostomus commersoni* (Lacépède).
Ptychocheilus oregonensis (Richardson) becomes *Ptychocheilus oregonense* (Richardson).
Acrocheilus alutaceus Agassiz and Pickering becomes *Acrocheilus alutaceum* Agassiz and Pickering.
Mylocheilus caurinus (Richardson) becomes *Mylocheilus caurinum* (Richardson).
Couesius plumbeus greeni Jordan becomes *Couesius plumbeus* (Agassiz).
Rhinichthys cataractae (Cuvier and Valenciennes) becomes *Rhinichthys cataractae* (Valenciennes).

Common names used are in most cases those recommended by the Joint Committee on Common Names of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists. Where these differ markedly from names used by Carl and Clemens (1953) the latter are included in brackets.

The following species are newly reported from British Columbia:

Platygobio gracilis (Richardson), flathead chub.
Percopsis omiscomaycus (Walbaum), trout-perch.
Cottus ricei Nelson, spoonhead sculpin.

The reference to *Pfrille neogaea* from Charlie Lake, British Columbia, by Wynne-Edwards (1952) is evidently attributable to a mistake in transcribing a list of specimen-localities from the Royal Ontario Museum of Zoology (Wynne-Edwards, personal communication).

Localities where each species has been taken are referred to by numbers which correspond to those in Figure 1. Details of these localities may be found in the Appendix. Numbers prefixed by "BC" refer to collection numbers of specimens in the Institute of Fisheries, University of British Columbia.

Records from the Mackenzie drainage of British Columbia are compiled for each species. Following the species list is a discussion of the general patterns of distribution of fishes astride the Fraser-Peace divide, and the probable routes by which fish have achieved these patterns.

Since the original preparation of this manuscript an additional species, *Hybognathus hankinsoni* Hubbs, has been taken in the British Columbia portion of the Mackenzie drainage. Discussion of this species has been inserted without alteration of the previous numbering system. *Coregonus coulteri* and *C. cylindraceus* were taken still later, and are discussed on page 789.

Family **Coregonidae**

1. *Coregonus williamsoni* Girard
MOUNTAIN WHITEFISH (Rocky Mountain whitefish)

Peace drainage: 2, 4, 8, 9, 10.
Liard drainage: 23, 24, 25. (36 specimens of *Thymallus arcticus signifer* from locality 17 are erroneously listed under *Prosopium williamsoni* by Bangham and Adams (1954).)

This whitefish has been reported from the western slope of the Rocky Mountains in the Nass, Skeena, Fraser and Columbia Rivers, south to the Truckee River in the Lahontan Basin of Nevada. On the east slope, Miller and Paetz (1953) have taken it in the upper basins of the Saskatchewan and Athabaska Rivers, and in the Peace River 130 miles east of the British Columbia border. It is not, however, recorded from Lake Athabaska or northward.

The mountain whitefish is evidently widespread in both the Peace and Liard drainages of British Columbia. The extension of its known range as far north as the Liard River places it close to the previously reported range of the round whitefish *Coregonus cylindraceus* Pallas. The latter species is stated by Wynne-Edwards (1952) to be one of the most universal of northern fishes, and is reported from the Yukon and Mackenzie systems as well as farther south and east. However, within British Columbia round whitefish have as yet been collected only from Teslin and Atlin Lakes on the Yukon River watershed[2]. Re-examination of specimens (BC54–254) reported as *Prosopium cylindraceum quadrilaterale*

[2]Now known from the upper Liard River. See Additional Species, page 789.

from Middle River (Takla Lake) on the Fraser drainage (Bangham and Adams, 1954) has shown these to be *C. williamsoni*. Gillraker counts of four specimens of *C. williamsoni* netted in Muncho Lake were 23 or 24, with lateral line scale counts 81 to 86.

Eschmeyer and Bailey (1955), give reasons for lumping *Leucichthys* and *Prosopium* with *Coregonus*. Many recent authors are in agreement, although Walters (1955) believes that *Prosopium* should be regarded as a distinct genus on the basis of juvenile parr marks and a single narial flap.

2. *Coregonus clupeaformis* (Mitchill)
LAKE WHITEFISH (common whitefish)

Peace drainage: 2, 12.

The species *C. clupeaformis* (*sensu lato*) ranges northwest from New England to the headwaters of the Yukon system. In British Columbia it occurs in the Yukon, Skeena and northern Fraser systems, and has been introduced in many more southerly localities. In the Mackenzie drainage of the province, the lake whitefish is recorded from Summit Lake and Swan Lake.

According to Walters (1955) the "humpback" form of whitefish from the Mackenzie system (figured by Wynne-Edwards (1952) as *C. nelsoni*) is properly called *C. clupeaformis*. Of the two distinct types of whitefish in Teslin Lake (Clemens, Boughton and Rattenbury, 1945) the humpback form is therefore also *C. clupeaformis*. Walters suggests that the somewhat low gillraker counts from Teslin may indicate a mixture of *C. clupeaformis* and the Alaskan humpback *C. lavaretus pidschian* (Gmelin). Indeed, the whole *C. clupeaformis* complex of North America may be conspecific with *C. lavaretus* of Eurasia and Alaska.

Family Thymallidae

3. *Thymallus arcticus signifer* (Richardson)
ARCTIC GRAYLING

Peace drainage: 6, 8, 12, Finlay and Parsnip Rivers (Haworth, 1917).
Liard drainage: 17, 20, 22, 23, 25, 27.

The Arctic grayling in North America extends from Arctic Alaska to the Mackenzie drainage, and southeastward to the Athabaska and Churchill Rivers. It has also been established in a few lakes of the North Saskatchewan drainage by stocking. In British Columbia it is found in the Yukon and Mackenzie systems. Grayling have also entered some of the northern drainages on the Pacific slope. They are reported from the Dezadeash River system, a tributary of the Alsek River, in Yukon (C. L. Anderson, personal communication), and from Tedideech Lake on the Nahlin River system, tributary to the Taku River in British Columbia (Walter Kirkness, personal communication). Arctic grayling are also reported from Cold Fish Lake in the upper Stikine system (T. A. Walker, personal communication), but have not been reported from any of the more southerly Pacific drainages. Nomenclature of this form is discussed by Walters (1955).

Family **Salmonidae**

4. *Salmo gairdneri* Richardson
RAINBOW TROUT (Kamloops trout) or STEELHEAD TROUT

Peace drainage: 2, 4, 5, 7.

S. gairdneri occurs in sea-run form on the Pacific coast north to Alaska, and has a landlocked form in the Alsek River in the southwest Yukon (Wynne-Edwards, 1952). Non-anadromous rainbow trout are widespread in the Columbia and Fraser systems. They are present in the upper Peace drainage at least as far downstream as Dawson Creek, where some are taken by anglers. Their presence there is at least partially attributable to numerous plantings of eggs from hatcheries in the southern section of the province. In Alberta they are native to the Athabaska drainage but were originally absent from the Saskatchewan drainage before fish cultural activities (R. B. Miller, personal communication). No species of *Salmo* is reported from the Liard section of British Columbia, or from Teslin Lake, or from the Mackenzie drainage below Lake Athabaska.

The subspecific categories usually applied to local salmonids contain contradictory elements. Thus two sympatric types of the salmon *Oncorhynchus nerka*, one anadromous and the other non-migratory, are sometimes assigned to the separate subspecies *O. n. nerka* and *O. n. kennerlyi*. On the other hand comparable sympatric coastal types of anadromous and non-migratory *Salmo gairdneri* are placed together in a single subspecies *S. g. gairdneri*. Parallel cases exist in *Salmo clarki clarki* and *Salvelinus alpinus malma* of coastal areas. Moreover, many of the taxonomic characters used to separate subspecies (e.g. *S. g. gairdneri*, *S. g. kamloops*, *S. g. whitehousei*) are now known to be at least partially phenotypic. Admittedly the patterns of variability are probably too complex ever to conform precisely to a formal system of nomenclature, which can therefore represent at best only an approximation to the actual relationships existing between populations. Nevertheless these contradictions in the present scheme of classification suggest the desirability of rejection of subspecific names in certain cases, such as the present, which do not appear to involve distinct allopatric races.

Some trout from Summit Lake resemble *S. clarki* in the possession of definite reddish-orange hyoid markings forming a broken stripe on either side of the isthmus. In all other characteristics examined, including a relatively short maxillary and the absence of hyoid teeth, they conform to *S. gairdneri*.

5. *Salvelinus alpinus malma* (Walbaum)
DOLLY VARDEN

Peace drainage: Peace, Parsnip and Finlay Rivers (Cowan, 1939).

The range of *Salvelinus alpinus* includes the whole of northern North America, extending south as far as northern California on the Pacific coast. Dolly Varden, *S. a. malma*, are probably found in every major watershed in British Columbia except the Okanagan. No specimens were available from the Mackenzie drainage, but Dolly Varden are reported to be taken in both the Peace and

Liard Rivers, and are large and abundant in the Parsnip. In Alberta they occur throughout the Peace, Athabaska and Saskatchewan River systems.

DeLacy and Morton (1943) have distinguished two species of char, *S. malma* and *S. alpinus*, in the Karluk drainage of Alaska. According to the diagnostic characters given by these authors, char of the northern Fraser drainage are more similar to *S. malma* than to *S. alpinus*. A specimen from Fraser Lake (BC54–499) has 21 pyloric caeca, 17 gillrakers, and numerous lateral spots, each smaller than the pupil of the eye. The whole arctic char complex is in need of taxonomic clarification; at present the writer follows Dymond (1947) and Carl and Clemens (1953) in regarding Dolly Varden as a subspecies of the wide-ranging species *S. alpinus*.

6. *Salvelinus namaycush* (Walbaum)
   Lake Trout (Great Lakes char)

Peace drainage: 2.
Liard drainage: 24.

The lake trout occurs in northern North America from Labrador to Alaska, south on the western slope as far as Shuswap Lake. Farther south it has been introduced in a few localities. It is found in the upper Taku system (Walter Kirkness, personal communication), in lakes of the upper Fraser and Skeena, in Teslin Lake, in the Liard system and in Lake Athabaska (Rawson, 1947). Lake trout are reported by anglers to occur in Arctic Lake at the headwaters of the Parsnip River. Reasons for placing this species, formerly *Cristivomer namaycush*, in the genus *Salvelinus*, are given by Morton and Miller (1954).

Family **Catostomidae**

7. *Catostomus catostomus* (Forster)
   Longnose Sucker (fine-scaled sucker)

Peace drainage: 2, 4, 5, 7, 9.
Liard drainage: 17, 18, 20, 21, 22, 24, 25.

The longnose sucker is distributed in North America from New England to Alaska, southward in the west to include the upper Missouri and upper Columbia basins. It occurs in the Yukon, Skeena and Fraser Rivers. It is abundant in both the Peace and Liard systems, and extends northward to the delta of the Mackenzie River. Subspecific status of British Columbia material has not yet been determined.

8. *Catostomus macrocheilus* Girard
   Largescale Sucker (coarse-scaled sucker)

Peace drainage: 2, 9.

This sucker has previously been reported as confined to the Pacific slope. It is recorded from the Skeena, Fraser and Columbia systems and coastal rivers in Washington and Oregon.

The range is now extended to include the upper Peace River as far downstream as the Alberta border. The significance of these and similar records in the Peace of species endemic to the Pacific slope is discussed later.

9. *Catostomus commersoni* (Lacépède)
WHITE SUCKER

Peace drainage: 2, 5, 9, 11, 12, 14, 15, 16.
Liard drainage: 17, 18.

White suckers extend from the Labrador peninsula and Hudson Bay drainage to the Mackenzie north as far as the Arctic Circle. They are not reported from the Yukon drainage. East of the Rockies they extend southward to South Carolina, Missouri and Colorado.

The species is abundant in both Peace and Liard systems in British Columbia. Recently white suckers have been identified from several lakes in the upper Fraser drainage as far south as Quesnel. Limited material from the Prince George area suggests that hybridization may have occurred here between *C. commersoni* and *C. macrocheilus*, and two apparent hybrids between these species were taken from Summit Lake. Both species are also recorded from the Skeena system. Additional collections are necessary to clarify the situation in regions occupied by these two allied forms.

Alteration of the specific ending in this and other species from "-ii" to "-i" follows the 1948 Paris decision of the International Commission on Zoological Nomenclature. (This decision was modified at Copenhagen in 1953; either ending is apparently now allowable, and the simpler is here followed.)

Family **Cyprinidae**

9a. *Hybognathus hankinsoni* Hubbs
BRASSY MINNOW

Peace drainage: 2.

The discovery of this species in Summit Lake north of Prince George is surprising. The natural range was previously described as extending from the Missouri River system east to the headwaters of the Hudson River, the nearest point to British Columbia in this range lying in eastern Montana (Bailey, 1954). Discovery of brassy minnows in the lower Fraser valley in 1952 (Carl and Clemens, 1953) was attributed to artificial introduction.

In 1955 a single specimen was taken by G. F. Hartman from Shelley Slough, an old ox-bow of the upper Fraser River eight miles northeast of Prince George. The following year the species was found in another small lake tributary to the Fraser River lying about 25 miles north of Prince George within two miles of the Mackenzie watershed. The same year, many individuals were taken in a warm creek entering Summit Lake on the Mackenzie drainage.

These collections extend the known range of the species some 400 miles northward, and raise some doubt as to whether the presence of the brassy minnow in British Columbia is the result of introduction by man. The closest

known sources from which specimens could have been artificially transported to the Prince George area are Montana and North Dakota, about 1000 miles distant, or, conceivably, the one known locality in the lower Fraser some 400 miles distant (provided they had previously been introduced to there). Furthermore, the present distribution requires that these fish subsequently were able to cross the continental divide, unless they were originally introduced into *both* the upper Fraser and upper Peace systems.

Such a series of coincidences is, of course, not impossible. Alternatively, the species may possibly occur naturally in the province, confined to a restricted type of habitat.

10. *Richardsonius balteatus* (Richardson)
REDSIDE SHINER

Peace drainage: 2, 4, 5, 9.

R. balteatus occurs in the Skeena and Fraser River, the coastal streams of Washington and Oregon, and in the Columbia system. Recent collections extend the range to the Peace drainage. In addition to those taken by Mr. I. Barrett and the author from the Peace River at the Alaska Highway bridge, specimens have been kindly supplied by Dr. R. B. Miller from within the Alberta border. These were taken on 16 August 1954 from the Wapiti River at Big Mountain Creek, approximately 50 miles east of the British Columbia boundary. As this locality is some 110 miles up the Smoky River system from its junction with the Peace, shiners have obviously become established over a large portion of the watershed.

The species is widespread and abundant in southern British Columbia; its adverse effect on the Kamloops trout sport fishery in Paul Lake has been strikingly shown by Larkin and Smith (1954). The impending invasion of more of the Mackenzie watershed by redside shiners is likely to affect some species of fish already present there.

The variable anal fin ray count of this species has received considerable attention. Eigenmann's (1895) claim of a negative correlation between altitude and ray count was discredited by subsequently published data. Lindsey (1953) demonstrated in British Columbia a positive correlation between ray count and water temperatures where young shiners were observed, but Weisel (1955) made comparable observations on the species in Montana and found there a negative correlation. In keeping with most questions involving meristic variation, this problem is not likely to be clarified until it is studied in the laboratory under controlled rearing conditions.

One feature of the pattern of anal fin ray variation in redside shiners is agreed upon by recent authors and is confirmed by collections from the Mackenzie area. Within comparable air temperature isotherms shiners have higher mean ray counts at more northerly latitudes. The three collections from the Peace drainage are from localities within the 12–15°C June–August isotherms. Their overall mean count (each locality given equal weight, sample sizes 64, 60 and 46) is 15.45 rays. More southerly collections within this temperature zone in

British Columbia average only 14.69 days, and collections from the northern United States average 13.10 (Lindsey 1953). Because of numerous complicating factors, the grouping of localities according to air temperature is crude. Nevertheless, over the entire range of the genus, ray counts so grouped show within each temperature zone a south-north increase. At least part of this trend is genetic, but McHugh (1954) and Vibert (1954) have recently shown that light can affect meristic characters in fish. As light shows a latitudinal cline in duration and intensity, its possible influence in the present case should not be overlooked.

11. *Ptychocheilus oregonense* (Richardson)
NORTHERN SQUAWFISH

Peace drainage: 2, 5, 9.

The genus *Ptychocheilus* is endemic to the Pacific slope, with four allopatric species. Three southern species occupy the Colorado, the Sacramento, and the Umpqua and Siuslaw drainages respectively. The northern species, *P. oregonense*, has been reported from the Skeena, Fraser and Columbia systems and from coastal streams of Washington and Oregon. Records from the Peace drainage in British Columbia now extend the range into the Arctic watershed.

Squawfish, largest New World members of the minnow family, have evolved as effective piscivores (Clemens and Munro, 1934) despite their lack of oral teeth. This evolution has occurred on the west slope of the continent, an area not inhabited by the northern pike, *Esox lucius*. Pike, predators well provided with teeth, appear to occupy somewhat the same ecological niche in the north and east which squawfish occupy in the west. Discovery of the squawfish in the Peace drainage discloses an area inhabited by both pike and squawfish. Presence of pike has not prevented the squawfish from spreading downstream at least as far as the Alberta border. Possibly habitat requirements of the two species are sufficiently unlike that the squawfish will eventually spread and share with the pike much of the Mackenzie basin. The impact of squawfish on the commercial fisheries of the large lakes of the Mackenzie such as Lake Athabaska might be appreciable.

12. *Margariscus margarita nachtriebi* (Cox)
NORTHERN PEARL DACE (Northern minnow)

Peace drainage: 14, 15, Fox Creek.

This minnow is distributed from Maine to Nebraska and northward to the tundra. Miller and Paetz (1953) report it from the Athabaska River drainage. The most westerly record is from Fox Creek (tributary to the Kiskatinaw River), 19 miles west of Dawson Creek, where one individual was collected by D. R. Hurn, F. P. Maher and the author on 29 July 1955 (BC55–220). A large individual (BC54–264) measured 155 mm. fork length (total length 6¼ inches).

13. *Mylocheilus caurinum* (Richardson)
PEAMOUTH CHUB

Peace drainage: 2, 5.

This is another species indigenous to the Pacific slope and formerly reported as occurring in the Columbia, Fraser and Skeena systems. Discovery of the peamouth chub in Summit and McLeod Lakes places it in a 50-mile stretch of the Peace River headwaters. None has been taken farther downstream.

14. *Chrosomus eos* Cope
NORTHERN REDBELLY DACE

Peace drainage: 14, 15.

The northern redbelly dace is found from the Maritime provinces to the Peace drainage and southward to Colorado. In Alberta it has been taken only in the South Saskatchewan and Missouri River drainages. It is unrecorded in that province from the Athabaska or Peace Rivers; in British Columbia it has been recorded only from Charlie Lake on the Peace system. It is abundant in this euthrophic lake, which appears to be the most northerly and westerly record of the species.

15. *Couesius plumbeus* (Agassiz)
LAKE CHUB

Peace drainage: 1, 2, 5.
Liard drainage: 18, 21, 22, 26.

The taxonomic status of the lake chub in British Columbia is in need of clarification, partially due to recent confusion in the literature resulting from the proposed amalgamation of the genus *Couesius* with *Hybopsis*. For the sake of clarity the nomenclature in the following discussion is that used prior to this proposed amalgamation, unless otherwise stated.

Three subspecies of *Couesius plumbeus* have been recognized in recent times (Dymond, 1947). East of the continental divide *C. p. plumbeus* (Agassiz) extends across Canada from New Brunswick to the delta of the Mackenzie; *C. p. dissimilis* (Girard) occurs to the south of this range and reaches from Michigan to the Missouri River. *C. p. greeni* Jordan is the western form occupying the Fraser and upper Columbia systems.

Previously unpublished records place the species also in the Peace and Liard systems in British Columbia. Lake chub are also reported from the upper Yukon system (Wynne-Edwards, 1952) in Yukon Territory, and specimens were taken in 1955 from the outlet of a warm spring draining into Atlin Lake in the Yukon headwaters, by R. G. McMynn and I. Withler of the B.C. Game Commission (BC55-205). None is reported from the lower Yukon system in Alaska.

As part of an effort to reduce unduly splintered genera, Bailey (1951a) placed the monotypic *Couesius* (along with several other genera) in the genus *Hybopsis*. Taylor (1954), who accepted this change, pointed out that the name

dissimilis was previously occupied by *Hybopsis dissimilis* (Kirtland) (formerly *Erimystax dissimilis*), and a new subspecific name must therefore be found for what was formerly *Couesius plumbeus dissimilis* (Girard). Unfortunately, lacking adequate data on the western form, Taylor stated that *Couesius greeni* Jordan seems to be applicable" and referred to the southernmost of the two eastern subspecies as *Hybopsis plumbea greeni* (Jordan). However, examination of British Columbia material from Mackenzie, Fraser and Columbia systems, and comparisons with specimens of both eastern subspecies from Eagle River, Michigan, kindly provided by Dr. R. M. Bailey, demonstrate that the equating of what were formerly *C. p. greeni* and *C. p. dissimilis* is erroneous.

In an assessment of the status of British Columbia specimens, material has been examined from 16 localities in the Columbia, Fraser and Mackenzie drainages. No clinal variation in taxonomic characters was noted across the province; scale count and fin size and shape varied irregularly between different populations. All British Columbia material has therefore been treated collectively in making comparisons with the two eastern subspecies.

According to published descriptions (Hubbs and Lagler, 1947), *C. p. plumbeus* and *C. p. dissimilis* are separable by the size and shape of the dorsal and anal fins. The former has long falcate fins, the latter shorter rounded fins. In British Columbia material the length of the dorsal (expressed as a proportion either of the head length or of the distance from occiput to dorsal origin) varies, between different populations, over the range of both other subspecies. Fin shape is moderately to markedly falcate in most populations, but in some collections all individuals have distinctly rounded fins. These differences may well be phenotypic, for they occur between collections from adjacent localities; moreover, the two collections with most markedly rounded fins (BC54–465, and BC55–205 from near Atlin Lake) are both from streams draining warm springs.

Eye size is another feature reportedly separating the two eastern subspecies. Eye diameter is large in most British Columbia material (greater than two-thirds the snout length); in this regard western specimens are unlike *dissimilis* and resemble *plumbeus*.

The scale count of the lateral line is the character most distinctive of British Columbia collections. Counts vary from 54 to 65 (mean 59.4 for 53 individuals), thereby lying almost completely outside of the published range of 64 to 72 for *dissimilis*. The stated range for *plumbeus*, 60 to 70, overlaps B.C. material considerably, but in every B.C. collection examined at least some individuals have scale counts below 60. Specimens from warm-spring outlets, although they resemble *dissimilis* in having rounded fins, are distinct from *dissimilis* in having low scale counts.

Trinomial designations in this species are evidently on an insecure footing, particularly as the two forms *C. p. plumbeus* and *C. p. dissimilis* occur together in some localities in the Great Lakes region, in contradiction to the usual concept that subspecies occupy geographically separate areas.

Bailey, Winn and Smith (1954) suggest that "a species is properly divisible into subspecies when data have been suitably published to demonstrate that it

consists of two or more allopatric populations, each displaying a high degree of uniformity over its range and differing with high constancy (a figure of at least 93 per cent of individuals is suggested) from other forms, each of which intergrades over a relatively narrow geographic area with at least one other form". Because such data are not available in the present case, the lake chub is best left without trinomial subdivisions. In the event, however, that further study should justify division into subspecies, their nomenclature would have to proceed from the following basis. The form occupying the western slope from Idaho northward through British Columbia to the Liard and upper Yukon systems should, if trinomials were adhered to, be referred to as *greeni*. This form perhaps intergrades in the Mackenzie system with *plumbeus* which extends eastward to the Atlantic. The third nominal subspecies extending from the Missouri River to Michigan south of the range of *plumbeus* has gone under the name *dissimilis*. As a further complication, if the suggested lumping of *Couesius*, *Erimystax* and other genera with *Hybopsis* (Bailey, 1951a) were followed, then this third subspecies could not be called *Hybopsis plumbea dissimilis* (Girard) because of prior occupation, could not be equated to *Couesius plumbeus greeni* Jordan for reasons stated above, and would therefore have to be given a new subspecific name.

The case against recognizing subspecies without further evidence has been stated above. The question of lumping the genus *Couesius* with the genus *Hybopsis* is quite separate, and has been decided here on the following grounds. Bailey (1951a) proposed this change but presented no supporting evidence. Such lack of published discussion, although unfortunate, is not in itself a reason for rejection of the proposal, for generic limits are in the final analysis decided solely by opinion. Moreover, the construction of larger genera as an indication of close relationships appears to be desirable in certain groups of fishes.

However, the uncritical acceptance of every proposal to lump genera would do as great a disservice to the usefulness of the binomial system as the acceptance of large numbers of monotypic genera. Lacking both first-hand knowledge of the eastern genera involved and published discussion of the case for and against, the present author has been unable to assess the proposed generic lumping, and has therefore retained the genus *Couesius* in the interest of nomenclatorial stability.

16. *Platygobio gracilis* (Richardson)
FLATHEAD CHUB

Peace drainage: 9, 10.
Liard drainage: 18.

The flathead chub occurs in the Mackenzie, Saskatchewan and Mississippi systems. The species has not been reported previously from British Columbia. Its discovery in both the Peace and Liard drainages is not surprising, as it has been recorded from the Mackenzie River at the Arctic Circle and from the Peace River 130 miles below the British Columbia border in Alberta (Miller and Paetz, 1953).

Bailey (1951a) proposed lumping *Platygobio* with *Hybopsis*. Reasons for this proposal are not yet published, and it is not followed here for reasons discussed under *Couesius plumbeus*.

17. *Rhinichthys cataractae* (Valenciennes)
LONGNOSE DACE

Peace drainage: 4, 9.
Liard drainage: 17, 18, 21, 22.

This species is distributed from coast to coast in Canada, north to the Arctic Circle in the Mackenzie River, and south as far as northern Mexico. In British Columbia it occurs in the Skeena, Fraser and Columbia as well as both Peace and Liard sections of the Mackenzie system. It has not been taken in the Yukon River drainage. Specimens from Jackfish Creek were unusually large, one having a fork length of 135 mm. (total length 6 inches).

Reasons for shortening the authorship of this species from "(Cuvier and Valenciennes)" are given by Bailey (1951b).

Family **Esocidae**

18. *Esox lucius* Linnaeus
NORTHERN PIKE

Peace drainage: 12, Peace River (Cowan, 1939), introduced from Swan Lake into Charlie Lake in August 1954.
Liard drainage: 17, 18, 27, Liard River and all the lakes adjacent (Dymond, 1936).

Northern pike occur in Canada from Labrador to Alaska, throughout the Mackenzie system, in the Yukon system (including Teslin Lake), and in the upper Mississippi Valley. The only report of pike in Pacific drainages is from the upper Taku drainage, in northwestern British Columbia (Walter Kirkness, personal communication). The distribution and relation of pike and squawfish have been mentioned previously.

Family **Percopsidae**

19. *Percopsis omiscomaycus* (Walbaum)
TROUT-PERCH

Peace drainage: 9, 10.
Liard drainage: 18, 21.

Trout-perch are distributed from the Hudson River to the Mississippi Valley, north to the Mackenzie drainage as far as the Arctic Circle, and in the Porcupine River in the Yukon River system.

The species has not been reported previously from British Columbia, but its discovery in the Peace and Liard drainages conforms to its known distribution. All four collections were from muddy moving water.

Family **Gasterosteidae**

20. *Eucalia inconstans* (Kirtland)
Brook Stickleback

Peace drainage: 14, 15.

The brook stickleback ranges from the Maritimes to the Peace system, and south to the Missouri system. In British Columbia it is recorded only from Charlie Lake and its outlet.

Family **Gadidae**

21. *Lota lota* (Linnaeus)
Burbot (ling)

Peace drainage: 12.
Liard drainage: 24.

Burbot are circumpolar in their distribution, ranging from Europe across northern Asia and northern North America to New England. Three subspecies have been generally recognized, *Lota lota lota* (Linnaeus) in Europe and most of north Asia, *Lota lota leptura* Hubbs and Schultz in eastern Siberia and Alaska, and *Lota lota lacustris* (Walbaum), formerly *Lota lota maculosa* (LeSueur) (see Speirs, 1952), in eastern North America.

If these subspecies are to be recognized, there should be evidence of three relatively homogeneous allopatric populations each connected with another by relatively narrow zones of intergradation. The opinions of Bailey, Winn and Smith (1954) in this regard have been quoted earlier in the discussion of *Couesius plumbeus*.

In *Lota lota*, morphological differences undoubtedly exist between the Alaskan form and, on one side the Eurasian form, and on the other the eastern North American form. However, comparison of published data combined with new material from the Mackenzie, Fraser and Columbia regions suggests that a composite of several intergrading populations is involved which is not in accord with present nomenclature. Evidence concerning the areas of intergradation between alleged subspecies is presented below.

Data on the zone of junction between *L. l. lota* and *L. l. leptura* comes largely from the Russian literature. Svetovidov (1948) gives the range of *L. l. lota* as extending eastward in northern Asia past the Lena River. *L. l. leptura* is stated to extend westward to the Kolyma River in northeast Siberia. The intervening area—the Indigirka and Yana River systems—is marked by queries on Svetovidov's distribution map. The range of variation of body proportions presented by him indicates mean differences but no clear-cut separation between the subspecies. Svetovidov suggests that if osteological distinctions between *L. l. lota* and *L. l. leptura* are not disclosed then possibly *leptura* should not be considered as a subspecies but only as a "natio" of *L. l. lota*.

In accord with the foregoing, Berg (1949) does not regard *leptura* as a full subspecies, but names the form in northeast Siberia, Alaska and northwest Canada as "*L. lota lota* natio *leptura* Hubbs and Schultz". The key character

which Berg gives to separate the latter form from *L. lota lota* (L.) is shape of the caudal peduncle. Even this distinction is less clear-cut than indicated by either Russian or American authors, for combination of data on 31 specimens of *L. lota lota* given by Svetovidov with those on 15 specimens given by Hubbs and Schultz (1941) produces a much greater overlap between the Eurasian and Alaskan forms than is shown by either publication separately (see Table I). Thus Berg's decision to place northeastern Siberian and Alaskan forms in the same subspecies as the Eurasian form is further strengthened. Unfortunately measurements are not listed separately for different localities by the Russian authors, but lack of a zone of sharp intergradation is suggested by the wide overlap in diagnostic characters, and also the geographic distribution of measurements in Table I. If, as seems probable, the 31 specimens listed by Svetovidov were collected from farther east, on the average, than the 14 from Europe listed by Hubbs and Schultz, then there appears to be a decided rise in peduncle ratio, within the range of "*Lota lota lota*", in populations approaching the geographic range of "*Lota lota leptura*".

Turning to the distinction between burbot of the northwestern and southeastern parts of their range in North America, more data are now at hand than were available to Hubbs and Schultz. These authors distinguished *leptura*, from both *L. l. lota* to the west and *L. l. lacustris* to the southeast, largely on the basis of a marked difference in the shape of the caudal peduncle. They stated that in other respects *L. l. leptura* appeared to agree closely with *L. l. lacustris*.

Alaskan and east Siberian specimens have long, narrow and acute posterior ends to the isocercal caudal region. This may be expressed as the distance from the notch behind the second dorsal fin to the posterior end of the vertebral column, divided by the distance between the notches at the ends of the dorsal and anal fins. Hubbs and Schultz' material showed little overlap in this character, except for three specimens from the Mackenzie, Fraser and Saskatchewan river systems which were designated as possible intergrades.

To supplement Hubbs and Schultz' data, measurements have been collected from several intermediate areas and are summarized in Table I. Several persons have generously allowed the inclusion of unpublished data in this table; Dr. W. B. Scott of the Royal Ontario Museum of Zoology supplied data on Fort Severn specimens, J. J. Keleher of the Central Fisheries Research Station measurements on specimens from Great Slave Lake, and Dr. W. A. Clemens measurements on specimens from Teslin Lake. Data from Robins and Deubler (1955) are also included. It should be pointed out that the separate listing in Table I of British Columbia collections tends to give them disproportionate emphasis in contrast to the lumped data from other larger areas.

Dr. C. R. Robins and Dr. Vladimir Walters, who have kindly examined the data in Table I, are both of the opinion that two allopatric groups are involved in North America, one originating from the Upper Mississippi and the other from the Yukon Valley. They feel that no true cline is apparent, and that zones of intergradation are sufficiently narrow to warrant subspecific differentiation. While this is evidently a debatable case with regard to nomenclature, I am per-

TABLE I.—Ratio of peduncle length to peduncle height (see text) in *Lota lota*.

Locality	Approx. Lat., °N	Approx. Long., °	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	No. of specimens	Mean	Source
New England	44–47	68–72W	1		1	4	5	7	7	5											30	1.39	Hubbs & Schultz
Susquehanna R.	42–43	75–76W			2	8	11	16	6	5	1										49	1.37	Robins & Deubler
Great Lakes–St. Lawrence	43–48	77–90W		1	2	10	13	5	13	3	3										50	1.36	Hubbs & Schultz
Labrador	54	62W		1				2	3	1	1										8	1.45	Robins & Deubler
Missouri R. system	39–46	95–108W					1	2	2	3	1										9	1.53	Hubbs & Schultz
Upper Mississippi	45–47	90–94W				1	7	8	2	3											21	1.40	Hubbs & Schultz
Waterton L., Montana	49	113W									1										1	1.75	Hubbs & Schultz
COLUMBIA SYSTEM, B.C.																							
Summit Creek, Creston	49	117W					1	2	4	1	2	1									11	1.54	BC55–33
Lower Arrow L.	49	118W						1													1	1.43	BC55–20
FRASER SYSTEM, B.C.																							
Shuswap L.	51	119W					1														1	1.34	BC55–279
Hawkins L.	51	121W					2	1	3	2	1	1									10	1.52	BC54–219, –222 & –225
Yellowhead L.	53	118W								1											1	1.63	Hubbs & Schultz
Tay Creek	54	122W								2	1										3	1.66	BC54–457
Cluculz L.	54	124W					2	3		1											6	1.42	BC54–132 and –166
Fraser L.	54	125W						1													1	1.41	BC54–499
James Bay	53	80W						1													1	1.36	Hubbs & Schultz
Fort Severn, Hudson Bay	56	87W										1	1								2	1.81	W. B. Scott
MACKENZIE SYSTEM																							
Muncho L.	59	125W							1			1									2	1.66	BC54–468
Great Slave L.	61	115W						1		2	2	2	3	2	2	7		1		1	23	1.99	J. J. Keleher
Fort Simpson	62	121W									1										1	1.73	Hubbs & Schultz
Teslin L.	59	132W				1				1	2	1	1								6	1.65	W. A. Clemens
Alaska	57–65	141–165W							1	1	2	4	4	5	3	1	2				23	1.93	Hubbs & Schultz
E. Siberia–N.W. Canada	?	?												X	X						7	—	Svetovidov
E. Siberia	69	161E								1		1	1		2	1	1				7	2.00	Hubbs & Schultz
Sakhalin	50	142E							1												1	1.47	Hubbs & Schultz
Europe and Siberia, to Kolyma R.	?	?					X	X	X	X	X	X	X	X							31	—	Svetovidov
Europe	45–65	0–20E			3	3	2	5	1												14	1.28	Hubbs & Schultz

sonally of the opinion that the evidence is ambiguous, that other historical interpretations are equally plausible, and that subspecific names are unjustified. This latter opinion is based on the following observations.

Peduncle ratio shown in Table I tends, within North America, to increase towards the north and towards the west; latitudinal and longitudinal trends are difficult to separate. A geographic dividing line drawn to best separate the data does not remove the appearance of clinal, or at least step-wise, variation, *within* each of the two areas separated. Ratios for specimens from the Missouri and upper Mississippi systems (west of 90°W) are distinctly higher than those from the Great Lakes, Susquehanna River, and New England areas (east of 90°W) (despite the fact that the Mississippi basin would be the most probable post-glacial source of repopulation from south of the ice sheet). Fraser and Columbia River counts average higher again than those from farther south and east; the two counts from Muncho Lake average still higher, while Great Slave Lake, Alaska and East Siberia have highest counts of all.

If, in this progression, the end populations are named as subspecies, these would have to be so restricted in range (in order to conform to the requirement of "relative homogeneity") that the area occupied by "intergrades" would be greater than that occupied by either named subspecies. The establishment of the present pattern by mixture of two stocks from either end of the North American range would require that genes from each end must spread an extremely great distance towards the opposite end.

Many collections of burbot in North American museums are not yet examined. Further measurements may in fact reveal a relatively smooth gradient across the continent, a gradation perhaps resulting from temperature or other environmental differences rather than from diverse parent stocks. A similar trend may exist in Europe and Russia. Alternatively, the present appearance of a series of irregular steps may be enhanced. Burbot are tolerant of low temperature and brackish water, and may very well have existed in several populations at the periphery of the ice sheet. Present patterns may therefore represent the outcome of a complex history of isolation and recombination from several centres. If so, more than two centres of distribution in North America seem to be indicated by the data at hand.

It is concluded that present evidence is insufficient for recognition of subspecific distinction between Alaskan and either European or eastern American forms. Without further data on what is evidently a complex situation, all should be referred to as *Lota lota* (Linnaeus). This is not to suggest that considerable morphological variation does not occur, but the use of subspecific names without further evidence is not only inconvenient, but also implies a particular form of step-wise distribution of variants which does not appear to exist.

Family **Percidae**

22. *Stizostedion vitreum vitreum* (Mitchill)
YELLOW WALLEYE (pike-perch)

Peace drainage: 13, 16.
Liard drainage: 18, 19.

The walleye ranges from Labrador to the mouth of the Mackenzie, and south to Virginia and to the Mississippi. It is not recorded from the Yukon system. It is probably widespread in both the Peace and Liard systems in British Columbia.

Family **Cottidae**

23. *Cottus ricei* Nelson
SPOONHEAD SCULPIN

Peace drainage: 10.
Liard drainage: 18.

This sculpin ranges from Quebec to the Saskatchewan drainage in southern Alberta, and north through the Mackenzie to its delta. It is unrecorded from the Yukon system.

The species, not previously reported from the province, was taken in both major drainages of the Mackenzie in British Columbia. Even the young may readily be separated from other species of sculpins in the region by the dense prickles, long curved preopercular spines and flat, spatulate head.

24. *Cottus asper* Richardson
PRICKLY SCULPIN

Peace drainage: 2, 3, 4, 5.

The prickly sculpin occurs in Pacific slope drainages from Alaska to California. On the British Columbia mainland it is recorded from the Columbia, Fraser and Skeena systems, and has been collected by T. A. Walker in 1954 from Cold Fish Lake at the headwaters of the Stikine River (BC54–485). Its recent discovery in the Peace system as far downstream as McLeod Lake now places it also in the Arctic drainage.

25. *Cottus cognatus* Richardson
SLIMY SCULPIN (mottled sculpin)

Peace drainage: 8, 10.
Liard drainage: 17, 21, 22, 23, 24, 25.

Cottus cognatus is the most widespread sculpin in North America, and may occur in eastern Siberia under the name *Cottus kaganowskii* Berg (Walters, 1955). It extends in the north from Labrador to Alaska, including the Mackenzie system down to Great Bear Lake and the Yukon system including Teslin Lake. It has also been taken in British Columbia from the Columbia and Fraser systems, and is now shown to be widespread in the Liard and Peace drainages.

Characters of 32 specimens from 8 localities in the Mackenzie drainage varied over the following ranges: dorsal spines rarely 7, usually 8 or 9; dorsal soft rays 15 to 18; anal rays rarely 9, usually 10 to 12; either one or two small spines below the principal preopercular spine; pelvic soft rays four, the fourth usually reduced (individuals with only three pelvic rays are common in the Fraser and Columbia systems but were not found from the Mackenzie system); lateral line ending below second dorsal fin.

Considerable variability occurs over this wide range, and further study may reveal that more than one species is involved.

DISTRIBUTION PATTERNS

The routes by which freshwater fishes have invaded British Columbia after the last glacial retreat can be investigated by examining their overall patterns of distribution. Carl (1950) outlined the probable mode of entry of most species in the province. Radforth (1944) attempted from the distribution patterns of fishes in Ontario to ascertain the centres of distribution from which species spread out at the close of the glacial era. Walters (1955) discussed avenues of dispersal of fishes in Alaska. These works have been drawn upon in the following discussion.

At the height of Pleistocene glaciation most of northern North America was covered by ice. Much of Alaska, however, was unglaciated, presumably as a result of low precipitation. Several species of freshwater fishes evidently spread east and south from Alaska following the glacial retreat; Walters (1955) pointed out that many of these probably originated from the Arctic slope of Alaska and of the Bering Strait land bridge, rather than from the Yukon Valley as has been commonly supposed. South of the ice sheet three major areas may be distinguished as later centres of distribution: the Pacific watershed from Washington south (with possible contributions from the Great Basin), the Mississippi basin extending westward to the continental divide, and the Atlantic coast drainage east of the Appalachian Mountains. A fifth source of repopulation by euryhaline fishes was from the sea.

Distribution patterns of species reaching the Fraser-Peace divide may be categorized broadly into four types which are illustrated in Fig. 2. Hatched areas are not meant to indicate detailed distribution records but merely the watersheds inhabited.

Type A. Ubiquitous Species

Several species are widespread both north and south of the Fraser-Peace divide. Of these the species-group *Salvelinus alpinus* occurs in both land-locked and sea-run forms; its taxonomy is confused, and it may have attained its present wide distribution via both freshwater and marine routes.

Three species, *Catostomus catostomus, Lota lota* and *Cottus cognatus*, have probably spread from Alaska; all occur or have close relatives in Siberia. Second centres of distribution may have existed in the upper Mississippi basin where each species now occurs. R. B. Miller (personal communication) points out that the absence of *C. cognatus* from most of the Saskatchewan River drainage strengthens the likelihood of two centres of dispersal for this species.

Two species, *Couesius plumbeus* and *Rhinichthys cataractae*, evidently originated from the southeast. The former occurs in only the upper part of the Yukon basin, into which it may be a comparatively recent migrant. *R. cataractae* is absent from the Yukon system. It is widespread west of the Mississippi and has probably redistributed from there (as well as, perhaps, from the Atlantic slope); it may have entered British Columbia via either the Columbia or the Mackenzie.

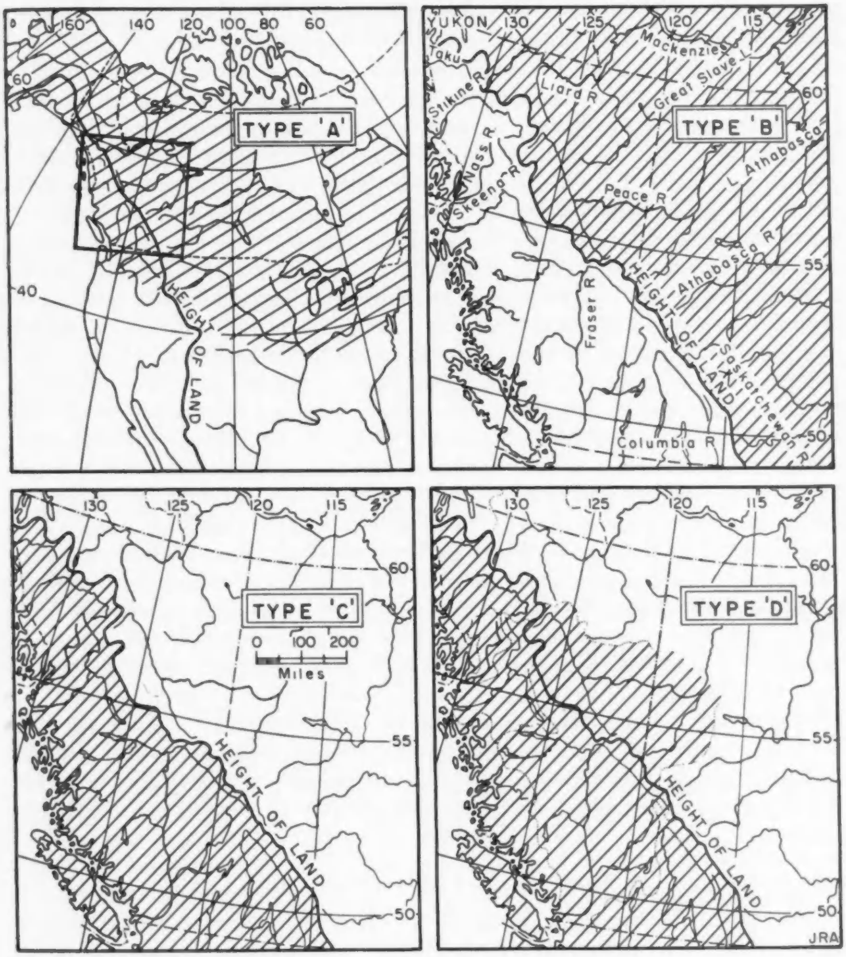

FIG. 2.—Distribution patterns of fishes reaching the continental height of land in British Columbia. See text.

Two species which occur in both Fraser and Mackenzie systems have probably entered from the north and do not completely occupy southern British Columbia. *Coregonus clupeaformis* and *Salvelinus namaycush* are, in the Fraser basin, native only to the northern portion, although both have been artificially distributed farther south. The former is absent from the Mississippi, while the latter is confined to its most northern waters. Their present ecological requirements suggest, however, that they may have originally occupied lakes along the ice front south of their present range. Walters (1955) believes that both species

originated from the Mississippi Valley rather than the Yukon Valley. Both have probably entered British Columbia via the Mackenzie.

One species, *Catostomus commersoni*, has evidently crossed the continental divide from north to south more recently, and thus has a unique distribution pattern in British Columbia. It is absent from the Yukon, and evidently followed the glacial retreat into northern Canada from either the Mississippi or Atlantic regions (or both). Despite its southern origin it has almost certainly invaded British Columbia from the north. Judging from its restricted distribution in the upper Fraser, this invasion has occurred comparatively recently, possibly due to human intervention. Further studies may indicate that it is insufficiently distinct from the Pacific species *C. macrocheilus* to prevent frequent hybridization when the two occupy the same territory.

The Pacific salmon, genus *Oncorhynchus*, are represented by five species on the Pacific slope of British Columbia, but none is reported from the Mackenzie system within the province. Both the chinook (spring) salmon, *Oncorhynchus tshawytscha* (Walbaum), and the chum (dog) salmon, *O. keta* (Walbaum), reach British Columbia in Teslin Lake via the Yukon River. The former is unrecorded from the Mackenzie, but *O. keta* has been taken as far up the Mackenzie system as Fort Smith above Great Slave Lake. The three remaining species, the pink salmon, *O. gorbuscha* (Walbaum), the coho salmon, *O. kisutch* (Walbaum), and the sockeye salmon, *O. nerka* (Walbaum), all occur in the lower Yukon River as well as in Pacific coast streams, but none reaches the Yukon headwaters in British Columbia. *O. gorbuscha* occurs in the lower Mackenzie, *O. nerka* has been questionably reported from there, while *O. kisutch* apparently does not reach the Arctic ocean.

The brassy minnow, *Hybognathus hankinsoni*, is now known to occur in the Mackenzie and Fraser systems as well as the Missouri and more easterly watersheds. Its sporadic occurrence in British Columbia may be the result of artificial introductions, although objections to this hypothesis have been mentioned previously.

Type B. Species Excluded from the Pacific Slope

A number of species occur in British Columbia only in the Mackenzie drainage and, in two cases, the Yukon drainage. *Platygobio gracilis, Percopsis omiscomaycus, Stizostedion vitreum vitreum* and *Cottus ricei* are probably each derived from the Mississippi centre of distribution. All four species are absent from the Yukon basin and extend into British Columbia only in the Mackenzie watershed. Three forms, *Chrosomus eos, Margariscus margarita nachtriebi*, and *Eucalia inconstans*, extend into British Columbia only in the vicinity of Dawson Creek, where they evidently reach close to the northern and western limits of their range. All three are probably derived only from the Mississippi area; representatives of *Margariscus margarita* occurring on the Atlantic slope represent a different subspecies. Limits to the northward extension of these species may be ecological rather than geographic. Radforth (1944) suggests that *Margariscus margarita* and *Chrosomus eos* in Ontario are restricted by minimal summer air

temperature isotherms, and such may be the case in northern British Columbia.

The remaining two species of Type B in the Mackenzie system, *Thymallus arcticus* and *Esox lucius,* are each found in Siberia as well as North America. *E. lucius* may have reached the Mackenzie from either the Mississippi or Yukon systems; *Thymallus arcticus* probably spread eastward from Alaska. Reports of these two species in the upper drainages of a few of the northern Pacific watersheds suggest that they have penetrated from east to west via the headwaters, but have evidently so far failed to reach the Skeena or Fraser.

Certain species not recorded from the Pacific slope reach British Columbia at the Yukon River headwaters but do not enter the province elsewhere. The broad whitefish *Coregonus nasus* (Pallas) (listed as *C. nasus kennicotti* by Wynne-Edwards, 1952, and as *C. kennicotti* by Clemens, Boughton and Rattenbury, 1945, (see Walters, 1955)), the cisco, *Coregonus sardinella* Valenciennes, the round whitefish, *Coregonus cylindraceus* Pallas, and the inconnu, *Stenodus leucichthys nelma* (Pallas) (see Walters, 1955 regarding subspecific name) all occur in the Mackenzie River outside British Columbia. The latter two may yet be found in the northeastern section of the province[3].

Type C. Species Restricted to the Pacific Slope

Certain species reach but do not cross the continental divide at the headwaters of the Fraser and Skeena Rivers. The white sturgeon, *Acipenser transmontanus* Richardson, occurs on the Pacific coast from Alaska to California. It ascends to the northern Fraser basin but has not been recorded from the Skeena. No species of sturgeon is reported from either the Yukon or Mackenzie system.

The following two Pacific slope species are restricted to freshwater and must have moved into British Columbia from the unglaciated areas to the south. The leopard dace *Rhinichthys falcatus* (Eigenmann and Eigenmann) was previously recorded only from Shuswap Lake on the Fraser system and from the Columbia system east of the Cascade range. Recent collections extend the range northward to the upper Fraser basin (Middle River near Takla Lake, and several points on the Fraser River between Prince George and Quesnel). This or an allied species has also been taken from the Vedder River in the lower Fraser Valley. *R. falcatus* has apparently spread northward from the Columbia, but has failed to penetrate to the Peace or, evidently, to the Skeena system.

Another species in this group is a sucker not previously described from British Columbia, either allied to or identical with *Catostomus columbianus* (Eigenmann and Eigenmann) of the Columbia system. This sucker has been taken from the Fraser system in the vicinity of Prince George as well as from the Columbia system in British Columbia, and is almost certainly derived from a southern centre of distribution.

The coastal cutthroat trout, *Salmo clarki clarki* Richardson, occupies the Skeena system right to the continental divide (Morrison Lake). It has probably reached the Skeena and smaller coastal river systems via the sea. No cutthroat trout are recorded from the Peace, Athabaska or North Saskatchewan drainages.

[3]See Additional Species, page 789.

The interior subspecies *Salmo clarki lewisi* (Girard), which has probably spread northward from the upper Columbia area, occurs naturally in the whole of the higher parts of the South Saskatchewan drainage including almost all the mountain lakes east of the continental divide (R. B. Miller, personal communication), as well as in the upper Missouri system and in the upper Columbia system in British Columbia.

A number of fishes listed by Carl and Clemens (1953) for British Columbia do not occur sufficiently far north or east in the province to reach the Mackenzie system and hence are not discussed here. These include some indigenous west slope species, such as the chiselmouth, *Acrocheilus alutaceum*, and the torrent sculpin, *Cottus rhotheus*, which extend across the United States border only in the Columbia system, some coastal species such as the eulachon, smelt and three-spine stickleback, and some artificially introduced species such as the eastern brook trout (speckled char), the carp, and several centrarchids.

Type D. Recent Invaders of the Peace System from the Pacific Slope

Five species have distribution patterns suggesting that they have penetrated from the Skeena or Fraser systems into the Mackenzie watershed in comparatively recent times. These are *Catostomus macrocheilus, Mylocheilus caurinum, Ptychocheilus oregonense, Richardsonius balteatus* and *Cottus asper*. All are present in the Columbia, Fraser and Skeena systems, all are absent from the Yukon, and all have been taken in the Mackenzie system only from the upper portion of the Peace drainage. All are present in Summit Lake (2, Fig. 1); *M. caurinum* and *C. asper* have not been taken below McLeod Lake (5, Fig 1), *C. macrocheilus* and *P. oregonense* have been taken just west of the Alberta border (10, Fig. 1), while *R. balteatus* has been taken 50 miles farther east. None is recorded from the Liard.

All five species are probably derived from the Columbia basin. *M. caurinum* and *C. asper* can enter salt water and might have ascended the Skeena River from its mouth; the other three evidently moved north via the Fraser River.

The restricted range of these species in the Peace system is probably attributable to their having crossed the height of land only recently, either by natural agencies or through introductions by anglers. Had they been present for a long period in the upper Peace, 'they would almost certainly have spread farther downstream. More extensive collecting may of course disclose some of these species elsewhere in the Mackenzie, but it is unlikely that largescale suckers, peamouth chub and squawfish would have escaped gill-net sampling during the Fisheries Research Board investigations of Athabaska, Great Slave and Great Bear Lakes. Furthermore, the Athabaska and Peace watersheds have been widely sampled in Alberta (Miller and Macdonald, 1950; Miller and Paetz, 1953).

An alternative explanation for the limited distribution of this group is that some physiological or ecological barrier prevents their downstream spread. Temperature might impose such a barrier, but this seems unlikely; certainly *C. asper* ranges farther north than the Peace River on the Pacific slope. The presence

of competitors or predators in the Mackenzie system might hold the spread of the immigrants in check, but would not likely serve as a permanent barrier.

Two final species, *Coregonus williamsoni* and *Salmo gairdneri*, also have probably originated on the Pacific slope but have achieved a wider distribution than the foregoing on the east slope of the Rockies. *C. williamsoni* occurs in the upper reaches of the Saskatchewan, Athabaska, Peace and Liard Rivers, suggesting multiple crossings of the continental divide. Radforth (1944) pointed out that *C. williamsoni*, which occupies both slopes of the Rockies, and *Salvelinus fontinalis* which occupies both slopes of the Appalachian Mountains, are each adapted to headwater streams which are liable to piracy from adjacent watersheds. *S. gairdneri* crossed the divide into the Athabaska system before the onset of fish cultural activities, although its present occurrence in certain east slope headwaters is attributable to artificial plantings.

DISCUSSION

Of 31 species reaching the divide at the Peace River headwaters, 13 have failed to cross it (except for the Arctic grayling and northern pike which have crossed into a few northern Pacific slope headwaters). (These figures exclude the anadromous Pacific salmon.) Ten are restricted to the east side and 3 to the west. Of the remaining 18 species which occupy both the Peace and Fraser Rivers, 7 have only limited distributions on the east slope and have presumably crossed from the west in fairly recent times, while 4 have limited distributions on the Pacific slope.

Ecological barriers may be responsible for a few of these range restrictions. The lake trout and lake whitefish have been only moderately successful when planted south of their natural range in British Columbia; both are well adapted to subarctic conditions, and may approach the present southern limit of optimal conditions for their survival on the Pacific slope. On the other hand *M. margarita*, *C. eos* and *E. inconstans*, which are adapted to warmer water, approach their northern limit in Charlie Lake. The scarcity of suitable habitats for these latter species close to the height of land may have reduced the likelihood of their involvement in headwater piracy.

The distributions of most other species in the area discussed are probably the result of mechanical barriers, or the lack of them, imposed by the topography. With the exceptions noted, those species having restricted distributions on one or other slope are probably recent immigrants still in the process of dispersal.

Some of the species which are widely distributed on both sides of the divide may have crossed at the headwaters during the cessation of the last glacial era. Large areas north and west of Prince George comprise glacial lake deposits; at least three major glacial lake basins were formed by the melting of the last ice sheet which covered the Nechako plateau (Armstrong and Tipper, 1948). Most of these old basins now lie within the Fraser watershed, but their outlets were probably at one time to the north instead of to the south.

More recent migrants have perhaps crossed when deposition of deltas, cutting back of headwater streams, or damming by log jams or beavers, have

reversed the direction of flow of streams of lakes astride the divide. Mountainous terrain, violent flooding and deep beds of glacial till in the valley bottoms all contribute to instability of water courses in the region. (The Stanwell-Fletchers (1943) refer to diversion of the Driftwood River 3 miles from its original course within living memory.) In addition, extremely low elevations and short distances separate headwaters of the Peace from those of the Skeena or Fraser at many points; a glance at a topographic map suggests several possible points for headwater piracy or for flooding of intervening low land. The same ease of headwater interchange pertains between the Skeena and Fraser systems, and at least 11 species intolerant of salt water are common to the two. In cases of apparently recent invasions, there is also the possibility of artificial introductions by anglers.

The number of species of fishes in northern British Columbia is small; their ranges are in many cases in a state of expansion. Apparently mountains have served as a check but not an insurmountable obstacle to this expansion; climatic and topographic instability inherent in mountainous terrain have provided intermittent passages through the barrier. Although the area has been habitable to fishes for only a short time (geologically speaking), yet as many species have crossed the continental divide as have been stopped by it. Distributional patterns suggest that many of the species which have found passage between the Pacific and Arctic drainages in Canada have done so via the Peace River in northern British Columbia.

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APPENDIX

Numbers preceding localities are those shown in Fig. 1 and referred to in the text. Following the latitude and longitude are collection numbers with date of collection and species taken (indicated by numbers given to species in text). Unless otherwise indicated, collections were made by C. C. Lindsey and P. A. Larkin, using either seines or rotenone, or, in Muncho Lake, gill-nets. The letters BC preceding collection numbers refer to specimens in the Institute of Fisheries at the University of British Columbia, Vancouver; P.M. refers to specimens in the Provincial Museum, Victoria.

1. Pond, west side Hart Highway, tributary to Summit Lake.
   122° 38′ W., 54° 15′ N.
   BC54–458 (8 Aug. 1954)–15.
2. Summit Lake, tributary to Crooked River.
   122° 40′ W., 54° 17′ N.
   BC54–459 (8 Aug. 1954)–7, 8, 9, 10, 11, 13, 15, 24.
   BC56–362, BC56–363 (C. C. Lindsey and G. H. Geen, 16 June 1956)–1, 2, 4, 6, 7, 8, 9, 9a, 10, 11, 13, 15.
3. Heart Lake, tributary to Crooked River.
   122° 37′ W., 54° 25′ N.
   BC54–230 (T. G. Northcote, 2 Aug. 1952)–24.
4. Angusmac Creek, tributary to Crooked River (referred to as "Swamp Creek" by Bangham and Adams (1954), and as "tributary of the Crooked River 50 miles north of Prince George" by Carl and Clemens (1953)).
   122° 42′ W., 54° 34′ N.
   Carl and Clemens 1953–7, 10, 17, 24;
   Bangham and Adams 1954–1, 4, 7, 10, 17, 24.
5. McLeod Lake, tributary to Parsnip River via Pack River.
   122° 57′ W., 54° 54′ N.
   BC54–477 (14 Aug. 1954)–4, 7, 9, 10, 11, 13, 15, 24.
6. Nation River, tributary to Parsnip River.
   122° 30′ W., 55° 31′ N.
   Robertson 1907–3.
7. Azouzetta Lake, tributary to Parsnip River via Misinchinka River.
   122° 37′ W., 55° 23′ N.
   BC54–101 (T. G. Northcote, 7 Aug. 1952)–4, 7.
8. Headwaters of Pine River, tributary to Peace River.
   122° 28′ W., 55° 32′ N.
   BC54–187 (T. G. Northcote, 7 Aug. 1952)–3.
   BC54–476 (14 Aug. 1954)–1, 25.
9. Peace River at mouth of Pine River.
   120° 41′ W., 56° 8′ N.
   BC54–461 (I. Barrett and C. C. Lindsey, 10 Aug. 1954)–1, 7, 8, 9, 10, 11, 16, 17, 19.
10. Peace River, south bank at Alaska Highway bridge.
    120° 39′ W., 56° 8′ N.
    BC54–460 (9 Aug. 1954)–1, 16, 19, 23, 25.
11. Pouce-Coupé River, tributary to Peace River.
    120° 3′ W., 55° 33′ N.
    Cowan 1939–9.
12. Swan Lake, drained by Pouce-Coupé River; also its tributaries Tupper and Meadow Creeks.
    120° 1′ W., 55° 31′ N.
    Cowan 1939–2, 3, 9, 18, 21.
    P.M.59–2; P.M.84–3; P.M.29 and P.M.30–9; P.M.81 and P.M.85–18.
13. Kiskatinaw River, tributary to Peace River.
    120° 32′ W., 55° 44′ N.
    Carl 1945–22.

14. Stoddart Creek, outlet of Charlie Lake, tributary to Beatton River.
    120° 55′ W., 56° 16′ N.
    BC54–119 (T. G. Northcote, 4 Aug. 1952)–9, 14, 20;
    BC54–475 (13 Aug. 1954)–9, 12, 20.
15. Charlie Lake, tributary to Stoddart Creek.
    120° 0′ W., 56° 20′ N.
    P.M.14 to P.M.17–9;
    BC54–27 (T. G. Northcote, 4 Aug. 1952)–9, 12;
    BC54–135 (T. G. Northcote, 5 Aug. 1952)–9;
    BC54–264 (Collector? 1953)–12;
    BC54–474 (13 Aug. 1954)–9, 12, 14, 20.
    Dymond 1936–16 (as *Chrosomus erythrogaster*).
16. Beatton River, tributary to Peace River.
    122° 34′ W., 57° 5′ N.
    Carl 1945–22;
    BC54–473 (13 Aug. 1954)–9.
17. Jackfish Creek, tributary to Prophet River.
    122° 40′ W., 58° 34′ N.
    BC 54–12 (J. A. McCabe, 30 Sept. 1953)–3, 18, 25;
    BC54–472 (12 Aug. 1954)–3, 7, 9, 17, 25.
18. Muskwa River, tributary to Fort Nelson River.
    122° 39′ W., 58° 47′ N.
    Carl 1945–22;
    BC54–471 (12 Aug. 1954)–7, 9, 15, 16, 17, 18, 19, 23.
19. Klua Lakes, tributary to Fort Nelson River.
    122° 15′ W., 58° 7′ N.
    Carl 1945–22.
20. Raspberry Creek, tributary to Muskwa River.
    123° 19′ W., 58° 54′ N.
    BC54–462 (11 Aug. 1954)–3, 7.
21. Kledo Creek, tributary to Muskwa River.
    123° 32′ W., 58° 50′ N.
    BC54–463 (11 Aug. 1954)–7, 15, 17, 19, 25.
22. Mill Creek, tributary to Tetsa River.
    123° 58′ W., 58° 40′ N.
    BC54–464 (11 Aug. 1954)–3, 7, 15, 17, 25.
23. Toad River, tributary to Liard River.
    125° 28′ W., 58° 49′ N.
    BC54–470 (12 Aug. 1954)–1, 3, 25.
24. Muncho Lake, tributary to Trout River.
    125° 47′ W., 59° 0° N.
    BC54–468 (12 Aug. 1954)–1, 6, 7, 21;
    BC54–469 (12 Aug. 1954)–6, 25.
25. Liard River at Alaska Highway bridge.
    126° 5′ W., 59° 24′ N.
    BC54–467 (11 Aug. 1954)–1, 3, 7, 25.
26. Swampy lake below Liard Hot Springs, also cool spring-fed tufa pools on hill side.
    BC54–465 (11 Aug. 1954)–15;
    BC54–466 (11 Aug. 1954)–15.
27. Dease Lake, tributary to Liard River via Dease River.
    Green 1891–3;
    Dymond 1936–18;
    Carl and Clemens 1953–3.

ADDITIONAL SPECIES

Since submission of this manuscript, two additional species of coregonid fishes have been taken in the upper Liard drainage in British Columbia. These were collected by C. C. Lindsey, E. H. Vernon and J. Dowsett in August 1956.

Coregonus coulteri Eigenmann and Eigenmann
PYGMY WHITEFISH (Coulter's whitefish)

Liard drainage: Dease Lake (locality 27).

Published records of pygmy whitefish are from the Columbia River system, from some Pacific drainages in Alaska, and from Lake Superior. Recently the species has also been taken in the Fraser River system (Cluculz Lake west of Prince George) and the Skeena River system (Maclure Lake southeast of Smithers), but collection of young specimens in seine hauls in Dease Lake constitutes the first record of pygmy whitefish from the Mackenzie River drainage. Eschmeyer and Bailey (1955) state that probably *C. coulteri* was a common and continuously distributed species near the periphery of the ice in late Pleistocene time; its present distribution represents a few relict populations which differ little morphologically from one another.

Coregonus cylindraceus Pallas
ROUND WHITEFISH

Liard drainage: Liard River (locality 25), Simmons Lake (30 miles west of McDame, tributary to Dease River), Dease Lake (locality 27).

Round whitefish, previously mentioned under the discussion of *C. williamsoni*, were found to occur together with the latter species in three localities. *C. cylindraceus* has not been recorded previously from British Columbia outside of the Yukon River drainage, but it is known to occur in northern Asia and northern North America from the Yenesei River in Siberia east to New England. Its distribution is of Type B, for it is apparently absent from all Pacific slope drainages except the Alsek River, into which it, like the arctic grayling and northern pike, has probably penetrated by headwater capture.

Reasons for dropping subspecific names in this species are given by Walters (1955).

Acetone–Water Mixtures for the Extraction and Rapid Estimation of Fats of Biological Materials, Particularly Fish Products[1,2]

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ABSTRACT

The variation of the efficiency of acetone as an extractant of fats from biological materials has been studied. The moisture content of the acetone was found to be the dominating factor. Refluxing time, as well as the ratio of solvent to sample, have been found to be of minor importance. A rapid, precise analytical method of fat determination based on these observations has been developed.

INTRODUCTION

Most methods described in the literature for extraction of fats from biological materials require special preparation of samples. With water-immiscible solvents, close attention must be given to drying, mixing with water-absorbing chemicals or treatment with strong mineral acids (A.O.A.C., 1955). It has been noted in the literature (Stansby, 1953) that acetone containing added water, mineral acids or organic acids, extracts more fat from fish meals than does pure acetone. However, no systematic exploration of the role of water in the extraction of fat by this solvent has so far been pointed out.

There is need for simpler, more reliable and more economical methods for the removal of fats from biological materials and for the quantitative determination of the fat content of such samples.

This paper reports an investigation carried out to determine the feasibility of using acetone as the extractant. Preliminary experiments showed that this solvent was more efficient than methanol, ethanol, or isopropanol (Harrison, 1938 and 1942) and that refluxing gave better results than continuous extraction in a Soxhlet apparatus. It was demonstrated that the water content of the acetone plays an important part in the extraction of fats. Taking this into consideration, a simple, rapid procedure was worked out for the removal of fats and determination of the amount of fat in wet as well as in dry materials. The efficiency and reliability of this method were tested. The procedure permits determination of "crude extract" which, for the purpose of this paper, is defined as acetone extractable material, and also "fat" which is the ethyl ether-soluble part of the crude extract. "Total fat" is the maximum amount of fat obtainable from a sample by repeated extraction.

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EXPERIMENTAL

For the sake of clarity, the final procedure is given first; it is then followed by a description of the experiments which led to its adoption.

Procedure

A sample containing approximately 0.5 g. of fat (usually 3 to 5 g. of fish meal or 5 to 25 g. of fresh tissue) is weighed into a 250-ml. flat-bottom, standard taper flask. Fifty ml. of first solvent is added (plus an additional 10 ml. for every additional gram of dry material for samples with a dry weight of more than 5 g.) and the mixture is refluxed for 30 minutes. The mixture is then filtered, with slight suction, through a medium or coarse sintered glass filter into a 125-ml. suction flask. The boiling flask and the residue are washed with about 30 ml. of acetone in small portions. The residue is then returned to the boiling flask and again refluxed with the same volume of second solvent.

For fish meals, the first solvent is dry acetone; the second, acetone with $30 \pm 5\%$ water. For fresh fish or other samples with more than 10% moisture, the first solvent is acetone with sufficient water added to make the water content of the liquid phase 20 to 30%; the second solvent is dry acetone.

While the second extraction is in progress, the first extract in the suction flask is evaporated to apparent dryness on a hot plate in a slow current of air. The fat of this crude extract is dissolved in 30 ml. of ether, added in four to six portions. The portions of ethereal solution are decanted into a tared, 50-ml. beaker, taking care not to entrain ether-insoluble material.

The second extract is treated in the same manner. The ethereal solution from it is combined with that from the first extract, and the ether is evaporated in a current of warm air. The fat is weighed after drying to constant weight, a procedure which may be conveniently achieved by heating the beaker two or three times, after removal of the ether, to 60°C. for 2 to 3 minutes and placing it, while still warm, in a vacuum desiccator for 5 to 10 minutes.

Materials

1. Fresh cod:	fillets.
2. Cod meal:	from fresh cod fillets, dried at a temperature not exceeding 50°C., then finely ground and stored in hermetically sealed containers; its water content remained constant (5.6%) for 6 months.
3. Fresh herring:	whole herring, moisture content 67.3%.
4. Herring meal:	the commercial product; 5 years old, moisture content 6.8%.
5. Fish sticks:	the commercial product.
6. Acetone:	reagent grade.
7. Ether:	ethyl ether, anhydrous, reagent grade.

Effect of the Water Content of Acetone on Fat Extraction

Samples of 5 g. of cod meal were extracted by two successive 4-hour refluxings, each with 100 ml. of acetone–water. The water content of the extractant

TABLE I.—Crude extract and fat obtained from 5 g. of cod meal in two successive 4-hour extractions, each with 100 ml. of acetone–water.

Amount of water in acetone	Yield of crude extract	Yield of fat
%(v/v)	*% weight of meal sample*	
0	4.7	3.7
1	6.0	3.5
2	6.4	3.2
3	5.9	3.0
4	6.5	3.3
5	6.9	3.6
8	8.3	3.7
15	11.3	3.9
20	13.3	4.0
25	15.3	4.0
30	17.4	4.0
40	18.9	3.9
50	24.3	3.5

was varied from 0 to 50% (v/v). After each refluxing, the weights of crude extract and fat were determined.

The results, given in Table I, show that maximum amounts of fat were obtained with acetone containing 20 to 30% water. With less water in the extractant, the yield dropped to a minimum for about 3% water, then rose again. The yield of crude extract increased with increasing water content. Extracts obtained with acetone containing up to 40% water were protein-free, as indicated by a negative biuret reaction; but with more than 40% water, the samples swelled considerably, were difficult to filter, and the extracts contained protein.

This experiment was repeated with 25-g. samples of fresh cod. Here the water content of the samples was taken into consideration for the calculation of the percentage of water in the extractant. The results, calculated on a moisture-free basis, were identical with those obtained with the dry material; again, maximum yields of fat were reached with 20 to 30% of water in the acetone.

TABLE II.—Yields of total fat obtained in the first and second extractions of cod meal with acetone containing various amounts of water.

Water content of acetone	Percentage of the "total fat" (4.0%) extracted		
	First refluxing	Second refluxing	Total
% (v/v)	%	%	%
0	83.3	9.1	92.4
1	79.3	8.6	87.9
2	73.7	7.6	81.3
3	66.2	8.5	74.7
4	73.7	9.1	82.8
5	82.3	7.6	89.9
8	86.9	7.6	94.5
15	94.7	4.5	99.2
25	97.4	4.0	101.4
30	97.0	3.0	100.0
40	95.5	2.1	97.6
50	69.2	18.7	87.9

The optimum amount of solvent was found to be 10 ml. per gram of dry material of the sample; yields were not increased with more than this amount.

Efficiency of Successive Extractions of Lean and Fatty Fish Meals

Samples of cod meal and of herring meal were extracted repeatedly with acetone containing various amounts of water. The amounts of fat extracted in the first and the second refluxing were expressed as the percentage of total fat, following the definition given in the introduction.

It is seen from Table II that the first extraction with acetone containing 10 to 30% water yielded 94 to 97% of the total fat of cod meal and that the second extraction brought the yield to 98 to 101%. For herring meal (Table III), these figures were 91.4 to 87.6% and 97.6 to 99.6%, respectively.

Table III.—Yields of total fat obtained in the first and second extractions of herring meal with acetone containing various amounts of water.

Water content of acetone	Percentage of the "total fat" (11.32%) extracted		
	First refluxing	Second refluxing	Total
% (v/v)	%	%	%
0	96.3	3.0	99.3
10	91.4	6.2	97.6
20	89.4	6.5	95.9
30	87.6	12.0	99.6
40	81.8	10.1	91.9
50	70.7	19.2	89.9

Refluxing Time

Several 5-g. samples of cod meal were refluxed repeatedly for different lengths of time with 50 ml. of acetone containing 30% water. The yields of crude extract and fat are listed in Table IV.

It is seen that refluxing twice for 30 minutes is sufficient. Extension of the refluxing period to 1 hour or more did not increase the yield. One 30-minute refluxing alone gave 97% extraction of the fat.

Table IV.—Effect of refluxing time and of repeated extraction with 50 ml. acetone, containing 30% water, on cumulative yield of crude extract and fat from 5-g. samples of a cod meal containing 4.0% total fat.

Extraction	Sample 1			Sample 2			Sample 3		
	Duration	Yield		Duration	Yield		Duration	Yield	
		Crude extr.	Fat		Crude extr.	Fat		Crude extr.	Fat
No.	*Hr.*	%	%	*Hr.*	%	%	*Hr.*	%	%
1	4	14.58	3.84	1	14.06	3.86	0.5	13.76	4.00
2	4	2.78	0.12	1	2.90	0.12	0.5	2.60	0.10
3	...	...	...	1	1.20	0.05	0.5	1.07	0.00
4	...	...	...	1	0.52	0.00	0.5	0.49	0.00
5	...	...	...	1	0.32	0.00	...	...	...
Totals	8	17.36	3.96	5	18.82	4.03	2	17.83	4.10

Periods shorter than 30 minutes were also tested. They gave lower yields with dried materials; but for fresh fish, 15 minutes was still sufficient. Thirty minutes was used in further tests.

Extraction with Dry Acetone as well as Wet Acetone

It was noted (see Table III) that in the first refluxing more fat was extracted from herring meal with dry acetone than with acetone which contained water. It was therefore investigated whether it would be advantageous to use dry solvent for one extraction and wet solvent for the other. The results obtained with cod meal and herring meal are given in Table V. Yields of 100% were obtained for both meals, if dry acetone was used first and acetone with 30% water second.

With fresh cod and fresh herring, yields of better than 98% were reached with acetone containing 30% water as the first extractant and dry acetone as the second.

Table V.—Efficiency of alternate extraction with wet and dry acetone of cod and herring meals.

Sample	First refluxing		Second refluxing		Total fat extracted[a]
	Water content of acetone	Fat extracted[a]	Water content of acetone	Fat extracted[a]	
	% (v/v)	%	% (v/v)	%	%
Herring meal	30	72.5	0	20.5	93.0
	0	93.0	30	7.0	100.0
Cod meal	30	90.0	0	2.5	92.5
	0	36.0	30	64.0	100.0

[a]As percentage of total fat content of the sample.

Reproducibility of Results

Using the finally adopted procedure: for dry samples dry acetone first, followed by wet acetone, and for moisture-containing samples wet acetone first, followed by dry acetone, replicate fat determinations were carried out on various materials. The results are given in Table VI. It is evident that the fat contents found in the replicate determinations agreed within very narrow limits.

Table VI.—Results of replicate determinations of the fat content of various samples, using the adopted procedure.

Replicate No.	Cod meal	Fish sticks	Fresh herring	Herring meal
	% fat	% fat	% fat	% fat
1	3.96	9.55	14.33	11.32
2	4.10	9.33	14.20	11.30
3	4.12	9.54	...	11.36
4	3.98	...	...	...

Comparison with Other Methods

The official A.O.A.C. methods for fat determination generally gave higher or lower results than the technique herewith described. A sample of cod meal containing 4% fat as determined by the proposed new technique was dried and

extracted for 16 hours with anhydrous ethyl ether in a Soxhlet apparatus (A.O.A.C. official method 22.25). Only 2.76% fat was extracted. An additional 16-hour period of extraction increased the result to 3.22%. An undried sample of the same material extracted by the same A.O.A.C. method and containing about 4% residual moisture gave only 1.7% fat extract. A sample of the same undried cod meal extracted by the A.O.A.C. method 22.28 using continuous extraction with acetone followed by acid hydrolysis gave 7.15% fat. That method considers the whole extract to be fat; however, after purification of the crude extract with ethyl ether, the result dropped to 3.7%. The high result obtained by acetone extraction only, may be explained by the fact that the amount of ethyl ether-insoluble material extracted by the acetone increases with the amount of moisture involved (Table I).

The results obtained from a commercial sample of herring meal were 11.3 and 9.9% for the proposed technique and the official A.O.A.C. method 22.25, respectively.

In the case of fresh fish materials the results were: From fresh cod fillets the proposed technique extracted 0.66% fat while the official A.O.A.C. method 18.9 (acid hydrolysis) extracted 0.61%. The same methods extracted from a sample of whole herring 14.3 and 13.9% fat, respectively.

DISCUSSION

The extraction of fat from fish materials with acetone containing various amounts of water showed that the yield of crude extract increased rapidly with the water content of the solvent. However, the ether-soluble part of the crude extract, namely the fat, did not follow the same pattern. The noticeable drop in fat extraction with acetone containing about 3% water (Table I) has been confirmed by several analyses of a similar cod meal.

The variability in the efficacy of acetone as a fat extractant may, at the first approach, be related to the hydration of the proteins. The results listed in Tables II and III show that the maximum amount of fat from cod and herring meals was extracted by two refluxings with acetone containing about 30% water. The figures listed in Table V, however, show that the same results could be obtained by using wet acetone in one only of the two refluxings.

For the analysis of fish meal the use of dry acetone as the first extractant was advocated because: (1) the time required for evaporation of the filtrate was considerably reduced; (2) fish meal initially partly defatted with dry acetone swelled more readily when treated with wet acetone, and penetration and extraction were thus enhanced; (3) separation of fat from crude extracts, obtained from spoiled meals, or meals prepared from spoiled raw material, was much easier.

In the case of fresh fish or wet fish materials, the protein has to be coagulated to prevent formation of gels, but not to such an extent that access of the acetone to the deeper imbedded fat would be impeded. This is achieved by adding to the wet sample sufficient acetone to make the water content about 30%.

Compared with other methods of fat extraction the proposed technique has the following advantages:

1. The time required for fat determination is considerably reduced.
2. The reproducibility of results is improved.
3. The sample does not require any special pre-treatment.
4. The size of the sample may be varied within wide limits according to its estimated fat content or the amount of material available.
5. The fat as well as the ether-insoluble fraction of the crude extract and the defatted residue are unspoiled and available for further examination.
6. The method does not require special equipment and is easily adapted to determinations in series.
7. The repeated refluxings provide an automatic check on the completeness of fat extraction.

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Fecundity of Wild Speckled Trout (*Salvelinus fontinalis*) in Quebec Lakes[1,2]

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CONTENTS

ABSTRACT

For the present macroscopic study over 1,000 female speckled trout from the Laurentide Park in Quebec have been examined. Of this number, 747 specimens received special attention. In ovaries of adult trout 3 types of eggs were found: *recruitment stock* (Class *a*), *maturing eggs* (Class *b*) and *atretic eggs* (Class *c*). In the process of maturation, the number of eggs of Class *b* progressively decreases due to atresia, but their diameter becomes greater. Comparisons

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[2]Contribution No. 51, Department of Fisheries, Quebec, P.Q. The colour plates illustrating this article have been provided by the Department of Fisheries of the Province of Quebec.

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of fecundity between different trout populations should be made only when eggs are nearly mature. The diameter of ripe eggs just previous to spawning, preserved in formalin, varied from 3.8 to 4.8 mm. There is a direct relation between the number of ripe eggs and the size of the fish: the extreme numbers of eggs were 90 and 4,800 eggs, and the extremes of fork lengths of females were 6 and 22 inches. The fecundity is greater among fish from lakes richer in food. A simplified method of determining the number of eggs in ovaries was devised. The maturity of females was determined by a 7-digit system. The colour of flesh was classified by a 6-digit system.

INTRODUCTION

In the Province of Quebec, the wild stock of speckled trout (*Salvelinus fontinalis*) is still found in great abundance. The author had the opportunity to direct for several years the Biological Station located in a great area of over 4000 square miles, known as the Laurentide Park, situated north of Quebec city. The abundance of local wild stock of speckled trout was demonstrated by a very generous daily bag limit, which was equal to 15 pounds plus one fish. The visiting tourists usually spent a few days in camps located near the fishing centres. For this reason, the author and his personnel had an exceptional opportunity to examine several thousands of fish.

Among different problems, the question of the fecundity of wild speckled trout received particular attention. The active studies on this subject were conducted at two different periods, from 1938 to 1941, and from 1949 to 1952.

MATERIAL AND METHODS

Characteristics of Region of Collections

Practically all of the trout collected for the present paper came from the Laurentide Park. The fish were caught in 36 different lakes and rivers. Due to their rather high elevation, from 1,000 to 3,000 feet above sea-level, the lakes in the Laurentide Park are subjected to quite a rigorous climate. The water is very soft, with hydrogen-ion concentration definitely on the acid side, varying from pH 4.5 to 6.8[3]. The typical geological formation found there is Precambrian (granite and gneiss).

The spawning season in cold lakes (Grand lac Jacques Cartier and des Neiges), situated above 2,500 feet, starts as early as August 20, while in other lakes it is typically limited to the month of September, with the greatest activity taking place during the first two weeks. The latest date for spawning in the Laurentide Park is about October 20[4]. Thus, the intensive growing season is rather short, varying from three to four months. In many lakes *S. fontinalis* is the only species of fish found.

[3]Other information on conditions in these lakes can be found in the manuscript report by Vladykov (1942a).

[4]In regions situated south from Quebec, spawning of *S. fontinalis* takes place much later. For instance, in southern Ontario, according to Ricker (1932, p. 99), speckled trout spawn from October 15 to December 15. However, as Hoover (1937), Hoover and Hubbard (1937), as well as Hazard and Eddy (1950) demonstrated, the spawning season of this species can be changed artificially by exposure to light.

Tagging recaptures of fish, ranging in length from 170 to 300 mm., showed that the yearly growth of local trout is very small, being on the average from 25 to 50 mm. only. Probably due to this fact, age determination by scales was found to be unsatisfactory[5].

Measurements and Preservation

The size of the fish referred to in this paper is only that of the *fork length*: it was measured from the tip of the snout to the extremity of the middle caudal rays. The length and weight were taken more often when fish were in a fresh condition.

The collected ovaries were preserved in 4 or 5% formalin for a period varying from a few months to one or three years. Although under the influence of this preservative the size of the ovaries and the diameter of the eggs are reduced slightly, this did not alter appreciably the results obtained. But it should be kept in mind that the maximum diameters of preserved eggs (over 4.5 mm.) are somewhat smaller than those in a fresh state.

Determination of Egg Numbers

Throughout this paper, unless otherwise indicated, the number of eggs was evaluated by the volumetric method, as described by Vladykov and Legendre (1940). Although this method, particularly in the case of eggs of small diameters, is subject to certain inaccuracies, and in spite of possible individual errors of several persons evaluating the egg numbers, it is sufficiently accurate for the purposes of the present study. In general, there are no cases in which the evaluated number deviated from the counted figure by more than 10%.

In order to compensate for any deformity due to preservation, the eggs were not measured individually. The usual procedure consisted in placing 20 eggs from each ovary in a row over a special measuring trough. The figure obtained was divided by 20. The general average, mentioned in our tables, was thus based on the combined averages of both ovaries, that is, calculated on a basis of 40

Table I.—Number of eggs, according to their diameter and size of the fish, for 747 females of *S. fontinalis* from different lakes, 1938–40 and 1949.

FL group (*mm.*)	Diameter of eggs in mm.											
	1.00–.99			2.00–.99			3.00–.99			4.00–.99		
	N	Mean	Range	*N*	Mean	Range	*N*	Mean	Range	*N*	Mean	Range
140–59	—	—	—	9	148	109–198	10	123	97–175	2	99	88–110
160–79	2	142	103–180	23	200	109–312	19	166	121–259	8	160	108–208
180–99	10	256	138–424	29	234	148–422	42	207	119–310	10	184	112–222
200–19	3	310	260–361	43	303	193–988	65	270	133–440	26	260	146–424
220–39	10	566	304–900	46	401	240–590	64	325	211–616	40	332	195–588
240–59	15	630	394–977	49	538	273–864	45	439	197–632	30	373	236–570
260–79	9	783	652–1044	27	670	438–966	24	530	288–831	10	416	318–571
280–99	7	1088	831–1585	18	722	446–1090	8	767	411–1218	3	770	581–763
300–19	7	1263	1041–1452	9	1047	762–1578	8	900	680–1271	8	993	632–1349
320–39	—	—	—	3	1260	1105–1565	2	973	961–985	1	900	—
340–59	—	—	—	—	—	—	3	1435	975–1666	—	—	—
Total	63			256			290			138		

[5]Ricker (1932) was able to "read scales" of the fish from Ontario, and Cooper (1951) of those from Michigan lakes.

TABLE II.—Comparison between the average number of eggs in ovaries and the number of eggs per 100 g. of fish weight, according to the size of females and the diameter of eggs. Data for 661 fish from different lakes, 1938–40 and 1949.

FL group (mm.)	Diameter of eggs in mm.															
	1.00–1.99				2.00–2.99				3.00–3.99				4.00–4.99			
	N	No. of eggs	Eggs per 100 g. Mean	Eggs per 100 g. Range	N	No. of eggs	Eggs per 100 g. Mean	Eggs per 100 g. Range	N	No. of eggs	Eggs per 100 g. Mean	Eggs per 100 g. Range	N	No. of eggs	Eggs per 100 g. Mean	Eggs per 100 g. Range
140–59	—	—	—	—	9	148	360	251–563	10	123	314	249–415	2	99	228	240–299
160–79	—	—	—	—	23	200	344	226–435	19	166	291	234–427	8	160	257	160–402
180–99	10	256	355	274–538	20	235	318	184–610	41	207	276	169–492	10	184	244	197–317
200–19	3	310	315	249–346	30	303	303	194–508	63	271	275	167–399	25	260	252	135–401
220–39	9	645	488	304–690	34	402	308	189–473	55	326	268	175–445	40	332	262	139–391
240–59	15	631	371	202–518	39	538	332	186–428	43	408	263	116–387	30	373	246	151–490
260–79	6	823	356	278–522	21	670	303	222–438	23	530	257	164–400	9	409	193	168–305
280–99	5	1104	432	318–672	13	736	273	193–345	7	767	293	172–397	3	678	273	231–376
300–19	7	1263	398	326–472	6	1047	310	251–331	8	900	269	203–355	8	959	286	202–442
320–39	—	—	—	—	1	1260	346	—	2	973	248	225–276	1	900	242	—
340–59	—	—	—	—	—	—	—	—	3	1435	289	280–371	—	—	—	—
Total	55				196				274				136			

eggs. Individual variation in diameter even of large eggs (3 or 4 mm.) from the same fish seldom exceeded 0.5 mm.

Extent of Material

Over one thousand female trout were examined for the present study. However, of these, only 844 fish are included in the following detailed account. These may be arranged according to egg diameter and year of capture, as follows:

Diameter of eggs (*mm.*)	Years of collection 1936	1938	1939	1940	1949	1951	Total
1.0–1.9	—	10	21	22	11	—	64
2.0–2.9	1	66	113	74	7	33	294
3.0–3.9	2	70	97	115	10	36	330
4.0–4.9	1	28	79	26	6	16	156
Total	4	174	310	237	34	85	844

For the sake of clarity, it should be stated that throughout the present paper the term "ova" is used as a synonym for maturing eggs.

Abbreviations

Throughout the present paper and particularly in tables, we shall use certain abbreviations, as follows:

Abbreviation	*Explanation*
Ave.	Average
Di.	Diameter of eggs in millimetres
F.	Total fish weight in grams, including viscera and gonads
F.L.	Fork length
N	Number (in statistical sense)
g.	Grams
O.	Weight of ovaries in grams
O/F	Weight of both ovaries in grams, expressed in percentage of the total weight in grams of a female, and called *maturity index*
mm.	Millimetres

REVIEW OF LITERATURE

The fecundity of speckled trout artificially reared in hatcheries has attracted the attention of a number of authors. Data have been published by von Bayer (1910), Hayford and Embody (1930), Hayford (1932), Russell (1935), Needham (1938), and Davis (1953), to mention a few.

On the other hand, it is rather surprising that the question of the fecundity of wild stock of *Salvelinus fontinalis* has barely been touched. In our earlier paper (Vladykov and Legendre, 1940), we were able to mention only three authors dealing with this subject: Titcomb (1897), Ricker (1932), and Stobie

(1939). During recent years, two more papers in this field[6] have been published, one by Smith (1947) and the other by Allen (1956). Smith (*loc. cit.*), on the basis of published records, supplemented by unpublished data furnished to him by several persons, was able to obtain information on only 53 wild and acclimatized speckled trout. Allen (*loc. cit.*) had for his study only 14 female trout from a Wyoming beaver pond. The most interesting data were given by Ricker (*loc. cit.*), who constructed a graph of the correlation between the length and fecundity of speckled trout. To his own records of 24 trout from Ontario, he added data on 29 fish[7] from Vermont by Titcomb (1897).

Ricker (*loc. cit.*) did not specify the exact diameter of the eggs in his material, but stated that "all counts were made of fish taken later in the year than August 1." As the spawning season in Ontario is at least one month later than in the Laurentide Park, we can reasonably assume that some of his fish had diameters of ova smaller than 3 mm. This probably explains[8] why Ricker's 22-inch trout from Lake Nipigon contained 5,630 eggs against 4,765 ova of 3.3 mm. in diameter in our fish of the same length from Lake Wayagamack, Que.

Apparently no author has dealt with the seasonal variation in the number of ova in *S. fontinalis* in relation to the eggs' diameter. As we shall see further in this paper, this problem is of prime importance to establish an accurate criterion of fecundity of trout from different areas.

Even such recent authors, as Määr (1949) or Grainger (1953), apparently were not aware that the numbers of eggs of very small diameters (0.1 mm.) and those of mature eggs (over 4.3 mm.), present in ovaries of Arctic char, are not comparable. On the other hand, Hickling and Rutenberg (1936), and Carbine (1944), used with success the diameter of eggs of different fish species to determine the type and duration of their spawning.

In conclusion, it is worthwhile to mention some excellent papers dealing with the spawning habits of speckled trout: Greeley (1932), White (1932), Schultz (1937), Hazzard (1938), and Smith (1941).

RIPENING CYCLE

In this section we shall deal only with the last phases of the ovarian cycle, when oocytes, present beneath the surface of the ovigerous lamellae, develop into mature ova. We do not know how much time is required in the case of *S. fontinalis* for oögonia to transform into oocytes. According to Meyen (1939), in *Perca fluviatilis*, for instance, this process requires nearly 3 years and in some sturgeons (*Huso*) from 16 to 18 years[9]. The increase in volume from oögonia to

[6]Carlander (1950, p. 53) did not give any new references on this subject.

[7]Titcomb, however, warns that in his material "some of these trout had apparently dropped part of their eggs before being captured."

[8]We have found that an individual fish contains more eggs in its ovaries at the beginning of the season than later in the year, as some of the eggs during maturation stopped to develop. Supplementary details will be found further in this paper.

[9]The above citation was taken from Suvorov (1948, pp. 205–208), as the original paper by Meyen was not available.

mature ova, in the case of perch (*Perca*), a species with small eggs (2 mm.), is about one million times. So, in the case of speckled trout this increase should be much greater.

The present work is based on a gross inspection of ovaries with either the naked eye or with a low-powered stereoscopic microscope[10].

Trout Ovaries

The structure of gonads in a female of S. *fontinalis* is typical for Salmonidae in general. It has two ovaries, often unequal in size, the right ovary most frequently being somewhat larger than the left one. Oviducts in our species, as in other Salmonidae (Berg, 1947, p. 425) are lacking[11].

The common belief has been that as the eggs of trout mature, they leave the ovary and fall into the body cavity. However, according to Kendall (1921) this is not the case, but the eggs when freed from the ovary collect in a trough, open on the dorsal side, formed by the extension of the peritoneal membrane surrounding the ovary. The troughs from the ovaries unite posteriorly on the upper side of the intestine to form a single "oviducal channel", which conveys the ova to the genital pore. Kendall believed that any eggs that accidentally get into the

Table III.—Reduction in the number of eggs per 100 g. of fish weight during maturation. The data in averages for the same 661 females, as those presented in Table II.

Egg diameter	N	Ave. diameter	Eggs per 100 g. of fish	
mm.		*mm.*	*No.*	%
1.00–.99	55	1.62	392	100.0
2.00–.99	196	2.52	317	80.9
3.00–.99	274	3.50	273	69.6
4.00–.99	136	4.25	251	64.0

Table IV.—Details concerning 343 females of *S. fontinalis* from selected localities.

Lake	Year	N	FL Range
			mm.
G.L. à l'Epaule	1938–39	20	141–207
G.L. à l'Epaule	1949	37	152–221
Long	1938–39	30	180–260
G.L. J.-Cartier (Head)	1938–39	90	168–320
G.L. J.-Cartier (3rd Rapid)	1938–39	37	141–288
Hermine	1938–39	47	175–316
Jupiter	1951	71	157–245
Grelon	1951	11	187–253
Total		343	141–320

[10]It is planned sometime in the future to supplement the present macroscopical study by detailed cytological work on the ripening cycle in Salmonidae.

[11]Weed (1934, p. 132), speaking about *Salvelinus alpinus* from Labrador, wrote "I caught sea-trout in salt water with free eggs in the oviducts". This erroneous statement of the existence of the oviducts in Arctic char was repeated by Sprules (1952, p. 12) and Grainger (1953, p. 363).

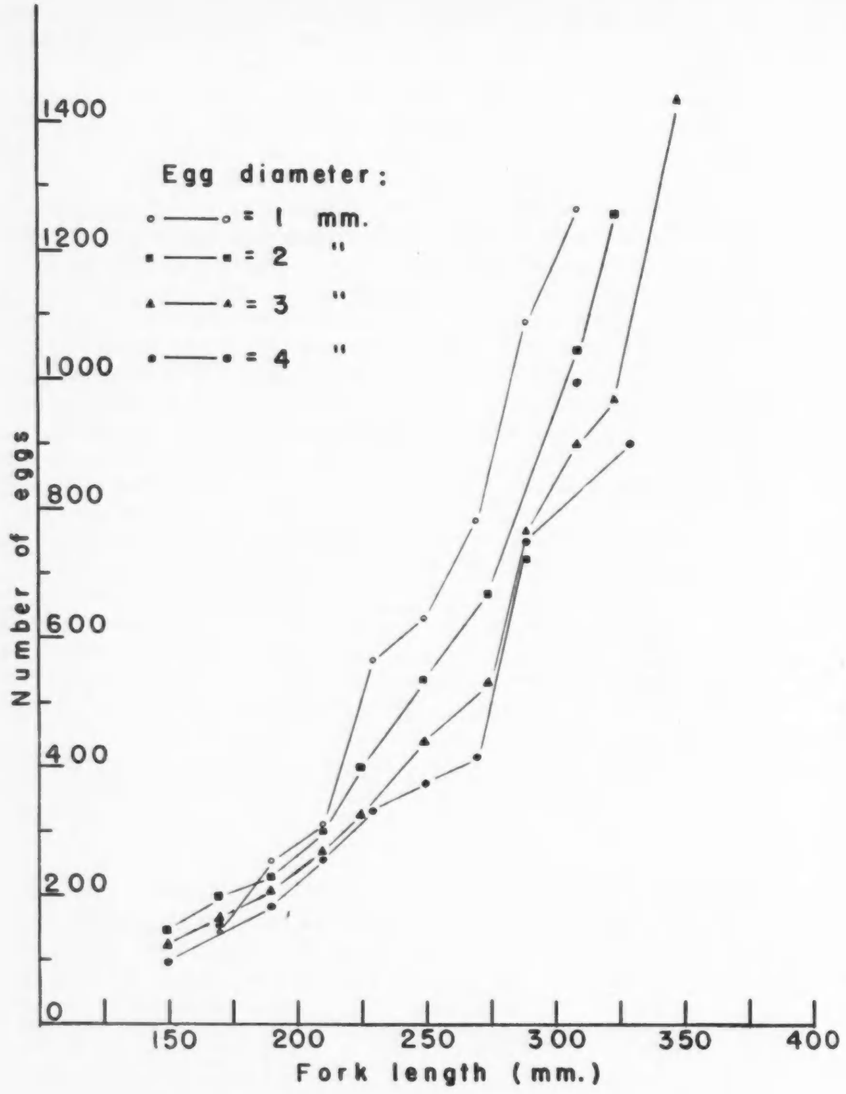

FIGURE 1.—Variation in number of eggs of 4 different diameters, according to the size of the fish. Data from the 747 females mentioned in Table I.

TABLE V.—Variation in the maturity index (O/F) according to the average diameter of eggs, for the same 343 females as presented in Table IV

Lake	N	Diameter of eggs in mm.																							
		4.00–4.49			4.50–4.99			1.00–1.49			1.50–1.99			2.00–2.49			2.50–2.99			3.00–3.49			3.50–3.99		
		N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F	N	Diam.	O/F
			mm.	%		*mm.*	%		*mm.*	%		*mm.*	%		*mm.*	%		*mm.*	%		*mm.*	%		*mm.*	%
G.L. à l'Epaule 1938–39	20	4	4.2	11.40	—	—	—	—	—	—	—	—	—	10	2.2	2.22	—	—	—	3	3.2	6.41	3	3.8	11.90
G.L. à l'Epaule, 1949	37	6	4.2	15.62	1	4.7	12.61	8	1.4	0.89	4	1.8	1.85	2	2.4	4.36	6	2.7	5.84	5	3.2	7.84	5	3.8	12.92
Long 1938–39	30	10	4.2	14.58	2	4.5	14.71	—	—	—	—	—	—	2	2.3	3.21	7	2.8	4.65	3	3.3	6.14	6	3.7	11.28
G.L. J.-Cartier (Head) 1938–39	90	26	4.2	12.17	12	4.6	14.69	—	—	—	2	1.9	1.56	2	2.5	4.10	7	2.8	4.19	16	3.2	6.63	25	3.7	9.04
G.L. J.-Cartier (3rd Rapid) 1938–39	37	19	4.2	13.54	2	4.6	15.07	—	—	—	—	—	—	—	—	—	—	—	—	5	3.4	6.74	11	3.8	9.61
Hermine 1938–39	47	4	4.2	14.96	—	—	—	8	1.3	1.02	7	1.7	1.15	3	2.3	2.20	4	2.8	4.10	14	3.3	7.84	7	3.8	10.09
Jupiter 1951	71	8	4.1	11.13	—	—	—	—	—	—	—	—	—	14	2.2	2.25	19	2.7	4.22	16	3.2	6.88	14	3.7	9.50
Grelon 1951	11	4	4.1	14.80	1	4.8	14.80	—	—	—	—	—	—	—	—	—	—	—	—	3	3.1	6.23	3	3.6	9.57
Summary	343	81	4.19	13.31	18	4.63	14.68	16	1.39	0.98	13	1.77	1.31	33	2.25	2.57	43	2.73	4.34	65	3.24	6.99	74	3.73	9.74

TABLE VI.—Number of eggs in both ovaries and number of eggs per 100 g. of fish weight, arranged according to the egg diameters. Data are in averages and referred to the same specimens as those mentioned in Tables IV and V.

Lake	Diameter of eggs in mm.															
	1.00–1.49		1.50–1.99		2.00–2.49		2.50–2.99		3.00–3.49		3.50–3.99		4.00–4.49		4.50–4.99	
	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.	No. of eggs	Eggs per 100 g.
G.L. à l'Epaule (1938–39)	—	—	—	—	215	274	—	—	131	273	149	302	142	225	—	—
G.L. à l'Epaule (1949)	336	472	348	509	246	412	263	423	262	337	237	340	206	293	141	197
Long	—	—	—	—	549	360	402	283	297	241	317	300	330	274	202	222
G.L. J.-Cartier (Head)	—	—	389	289	533	383	410	258	288	254	276	224	313	228	281	206
G.L. J.-Cartier (3rd Rapid)	—	—	—	—	—	—	—	—	257	229	327	247	366	262	364	270
Hermine	754	552	665	333	542	283	513	271	573	323	607	266	756	269	—	—
Jupiter	—	—	—	—	271	291	215	259	220	283	221	270	223	260	—	—
Grelon	—	—	—	—	—	—	—	—	297	274	300	276	314	276	248	234
Total		525		351		302		276		281		254		248		216

TABLE VII.—Fork lengths of 343 females and number of eggs per 100 mm. of fish length, arranged according to the egg diameters. Data are in averages and refer to the same specimens as those mentioned in Tables IV–VI.

Lake	Diameter of eggs in mm.															
	1.00–1.49		1.50–1.99		2.00–2.49		2.50–2.99		3.00–3.49		3.50–3.99		4.00–4.49		4.50–4.99	
	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.	FL	Eggs per 100 mm.
	(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)	
G.L. à l'Epaule (1938–39)	—	—	—	—	184.6	116	—	—	156.3	84	156.7	95	169.8	83	—	—
G.L. à l'Epaule (1949)	187.3	179	184.3	189	174.0	141	181.1	145	192.8	136	189.0	126	188.8	109	195.0	72
Long	—	—	—	—	243.0	226	231.6	174	224.7	132	212.7	149	227.1	145	206.0	98
G.L. J.-Cartier (Head)	—	—	225.0	173	237.5	224	241.0	170	215.4	134	220.1	125	235.3	133	234.6	120
G.L. J.-Cartier (3rd Rapid)	—	—	—	—	—	—	—	—	212.0	121	234.3	140	221.9	165	229.0	159
Hermine	232.3	325	247.9	268	231.7	234	245.0	209	247.0	232	260.6	233	298.5	253	—	—
Jupiter	—	—	—	—	206.3	131	198.3	109	193.0	114	198.2	111	213.6	93	—	—
Grelon	—	—	—	—	—	—	—	—	215.3	138	217.0	138	222.8	141	216.0	115
Total	209.8	260	224.8	233	204.2	152	212.6	147	212.4	152	229.9	131	227.4	143	227.6	

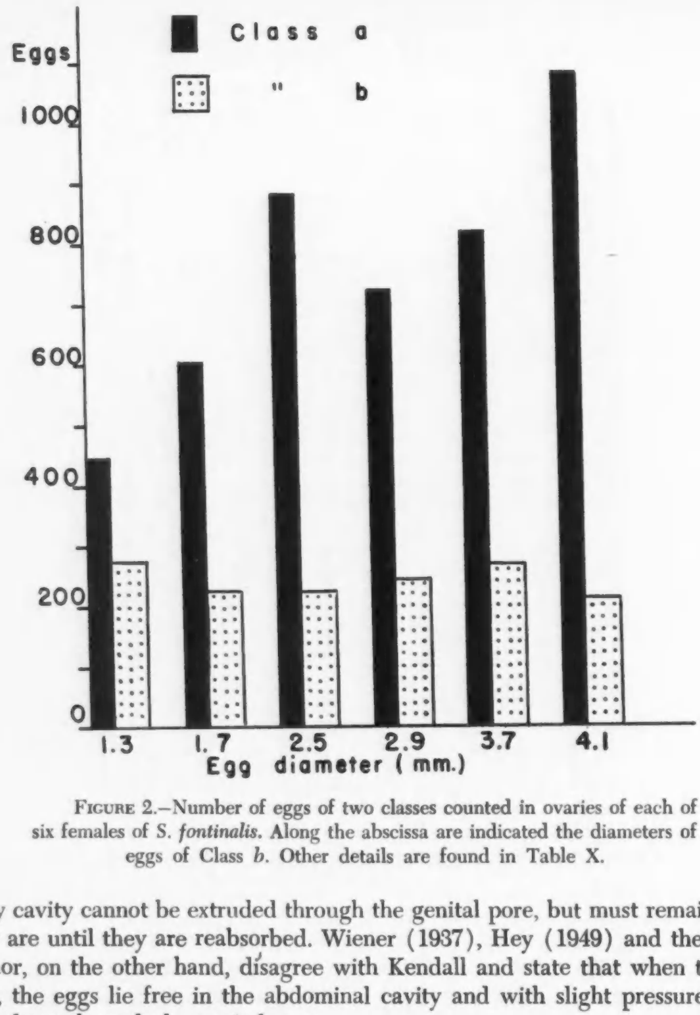

FIGURE 2.—Number of eggs of two classes counted in ovaries of each of six females of S. *fontinalis*. Along the abscissa are indicated the diameters of eggs of Class *b*. Other details are found in Table X.

body cavity cannot be extruded through the genital pore, but must remain where they are until they are reabsorbed. Wiener (1937), Hey (1949) and the present author, on the other hand, disagree with Kendall and state that when trout are ripe, the eggs lie free in the abdominal cavity and with slight pressure can be forced out through the genital pore.

The present author observed quite often in the body cavity of female trout, near the genital pore, a small number (1–6) of large ova left over from last year's spawning (Plate III). Even after a sojourn of 9–12 months in the body cavity, some of these eggs were not reabsorbed as yet. We found also in the body cavity of certain females some empty shells of ripe ova, which were left there after previous spawning.

The most striking case was that of a female, 405 mm. in fork length and weighing 725 g. which was caught in Lake Hélène (Camp Devlin) on September 18, 1938. It carried 1,205 ripe eggs, 4.4 mm. in diameter. Along its extended

COLOUR PLATES I, II, III

Plate I.—A female of S. *fontinalis* in Stage 1 of maturity, fork length being 176 mm. Ovaries contain numerous maturing eggs (Class *b*) of small diameter. This fish, as well as others on Plates II and III, were taken at the head of Grand lac Jacques Cartier, during September 1940.

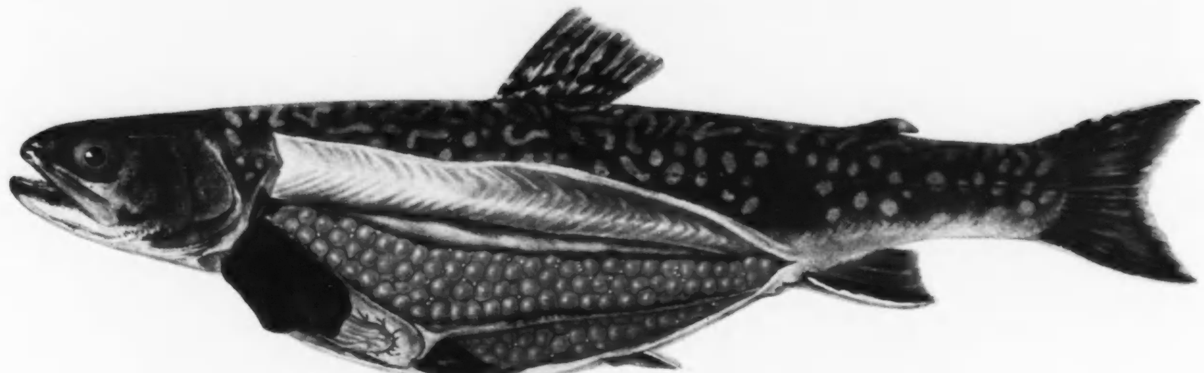

Plate II.—A female of S. *fontinalis* almost ready to spawn (Stage 5), fork length being 235 mm. Its ovaries bulged with ripe ova, among which are seen minute eggs of recruitment stock (Class *a*). Flesh is highly coloured (Stage 4).

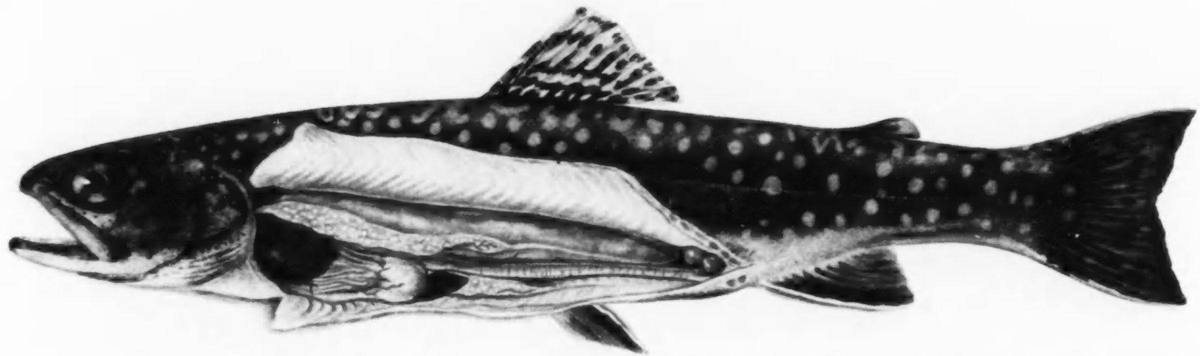

PLATE III.—A spent female of S. *fontinalis* (Stage 6), fork length being 216 mm. Ovaries are half shrunk and filled with eggs of recruitment stock (Class *a*). Near the genital pore are seen two mature ova, which were left over after spawning.

TABLE VIII.—Comparison between the diameter of eggs and their number per 100 g. of fish weight and 100 mm. of fish length, as well as the maturity index. The data are averages and refer to the same specimens as those mentioned in Tables IV–VII.

Egg diameter	N	Diameter	Eggs per100 g.		Eggs per 100 mm.		Maturity index	
mm.		*mm.*	*No.*	%	*No.*	%	*No.*	%
1.00–1.99	29	1.56	431	100.0	248	100.0	1.15	8.5
2.00–2.99	76	2.52	286	66.4	149	60.1	3.61	26.6
3.00–3.99	139	3.50	266	61.7	140	56.5	8.47	62.5
4.00–4.99	99	4.31	242	56.1	138	55.6	13.55	100.0

ovaries, from the liver to the anus, all available space in the body cavity was literally packed with flattened mature ova, left over from the previous spawning season, their number being 841. Lake Hélène is a small body of water, about 4 acres, very muddy, but rich in food. It is accessible to trout only early in spring through a trickle of a stream. During the summer and early autumn, this lake is completely isolated. For the few spawning trout found in it, there is no spawning bed at all. Thus our fish, in spite of being unable to shed mature ova in the autumn 1937, continued to develop new eggs in 1938, which would also not be laid. The burden of these numerous unspent eggs, stored over a year in the body cavity, apparently only slightly affected this female trout.

Types of Eggs

In the ovaries of a speckled trout, regardless of its age, eggs are always present. Under a low-powered microscope, even in ovaries of small, immature fish eggs of two different diameters can be distinguished. As our main work was of a macroscopical nature, we will disregard details on eggs of diameters smaller than 0.1 mm. In larger females, from 140 mm. on, usually three types of eggs are observed. These can be defined as follows:

Class *a*: *Recruitment stock* of small eggs, yolkless and transparent in fresh condition or opalescent in preserved material, present in clusters between eggs of Class *b*. The common diameter range of the recruitment eggs is from 0.1–0.9 mm.

Class *b*: *Maturing eggs*, loaded with yolk, yellowish in early stages to orange towards spawning, becoming progressively more transparent; spherical when fresh but often distorted by fixatives. They gradually decrease in number but increase in size, and thus become distinctly set apart from the remaining eggs. Apparently all maturing eggs which stop development become *atretic* (see Class *c*). The diameter of maturing eggs varies throughout the season from 1.0 to 4.8 mm.

Class *c*: *Atretic eggs*[12], i.e. the original maturing eggs, which stop growing and gradually degenerate, while the remaining eggs continue to develop into

[12]This term is taken by us from human histology. According to Maximow and Bloom (1947, p. 557), in the human ovary a dominating majority of original follicles does not reach the stage of mature ova, but gradually degenerates and disappears. This involution of a follicle is called *atresia*. Hence a degenerated fish egg can also be called *atretic*.

TABLE X.—Number of eggs of three classes present in ovaries of six females of *S. fontinalis*, taken in Grand lac à l'Epaule, 1949.

Date	FL	Stage of maturity	Number of eggs *a*	*b*	*c*	Diameter of Class *b* eggs
	mm.					*mm.*
VII, 14	191	1	443	275	—	1.3
VII, 14	197	1	604	231	5	1.7
VIII, 18	174	2	881	228	37	2.5
VIII, 18	192	3	725	248	29	2.9
IX, 13	191	4	820	271	14	3.7
IX, 13	197	4–5	1,087	214	8	4.1

mature ova. In formalin preserved material they are opaque or pure white in early stages, but become progressively darker, finally a dirty orange-tan, as degeneration proceeds. Their shape more or less irregular, usually elongated or flattened. Their diameters are from 1 to 3 mm.

Apparently the presence of atretic eggs in fishes was overlooked by previous authors. These eggs however, play an important role of a "safety valve". Early in the season, the maturing eggs (Class *b*) are very numerous. If one takes a female speckled trout in the early stages of maturity and calculates what that ratio in percentage of the ovarian weight to fish weight i.e. the *maturity index*, would be if no eggs degenerated, the result can be seen to be fantastic; thus the reason for the atresia. To illustrate this point, we shall discuss the following cases, for which we assume, that all maturing eggs (Class *b*) reach 4.3 mm. in diameter. These two female trout were taken in June, 1939:

Lake	Fish		Eggs		Weight of ovaries		Maturity index
	FL	Weight	Diam.	No.	Present	Calculated final wt.	
	mm.	*g.*	*mm.*		*g.*	*g.*	
Grand lac à l'Epaule	185	66.7	1.5	516	0.5	29.93	44.9
Lac des Chênes	270	200.2	1.5	1044	2.4	60.55	30.2

If in the above cases the original number of maturing eggs, 1.5 mm. in diameter, was not reduced at spawning time by atresia, then the maturity index would be from 30 to 45. In our material we never found a spawning trout with the index greater than 20.

The number of atretic eggs varies considerably with the season, locality, and probably food of the fish. Table XI contains information on 31 females from Grand lac à l'Epaule taken in 1949. As can be expected, the number of atretic eggs is particularly high early in the season, when Class *b* eggs begin to grow fast. When the maturing eggs attain diameters of 1.0–1.9 mm., the number of atretic eggs is at its height, being on the average 116. The maximum number of atretic eggs in Grand lac à l'Epaule material was that of 213, found in two

TABLE IX.—Reduction in the number of eggs (Class *b*) during maturation of females of *S. fontinalis* from Grand lac à l'Epaule, 1949.

Date	FL. range	Diameter range	*N*	Data in averages									
				FL	Diam.	No. of eggs		Eggs/100 g.		Eggs/100 mm.		Maturity index	
1949	*mm.*	*mm.*		*mm.*	*mm.*	*No.*	%	*No.*	%	*No.*	%	*No.*	%
July 14	165–207	1.2–1.9	8	186.4	1.46	353	100.0	505	100.0	189	100.0	0.91	7.19
Aug. 18	152–210	2.5–3.8	10	182.8	3.02	254	72.0	395	78.2	139	73.5	7.79	61.6
Sept. 14	166–211	3.2–4.7	7	188.4	3.98	214	60.6	297	58.8	113	59.8	12.65	100.0

TABLE XI.—Number of atretic eggs in both ovaries of trout from Grand lac à l'Epaule, taken from July 14 to September 14, 1949, the fork lengths of 31 females being 152–211 mm.

Diameter of eggs (*mm.*)	*N*	Number of atretic eggs								
		0	1–9	10–19	20–39	40–59	60–99	100–149	150–219	Average
1.0–1.9	12	—	1	—	—	3	2	2	4	115.8
2.0–2.9	6	—	1	2	3	—	—	—	—	20.2
3.0–3.9	7	1	3	2	1	—	—	—	—	8.3
4.0–4.9	6	1	3	—	2	—	—	—	—	10.0
Total	31	2	8	4	6	3	2	2	4	52.6

PLATE IV.—Dorsal view of ovaries with nearly ripe eggs (Stage 4 of maturity) from a female of *S. fontinalis*, 237 mm. in fork length, taken in Lake Bastion, near Quebec City, September 2nd, 1949. Among maturing ova (Class *b*) are seen numerous, small, round, white eggs of recruitment stock (Class *a*). Several atretic eggs (Class *c*) are present, some of which are indicated by small arrows. The large white arrow in this and other plates points towards the head.

this and other plates points towards the head.

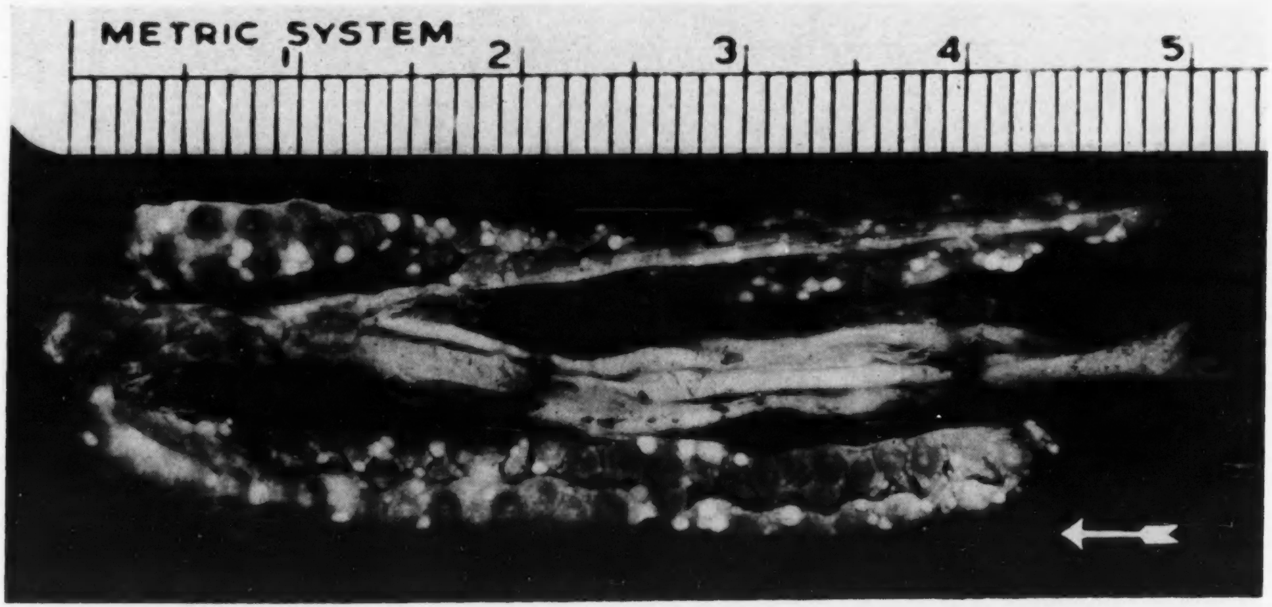

PLATE V.—Dorsal view of ovaries removed from a female of *S. fontinalis* in Stage 2 of maturity, the fork length being 195 mm. The fish was taken in Grand lac à l'Epaule, July 14th, 1949. Among maturing eggs (Class *b*) are seen many white roundish atretic eggs (Class *c*).

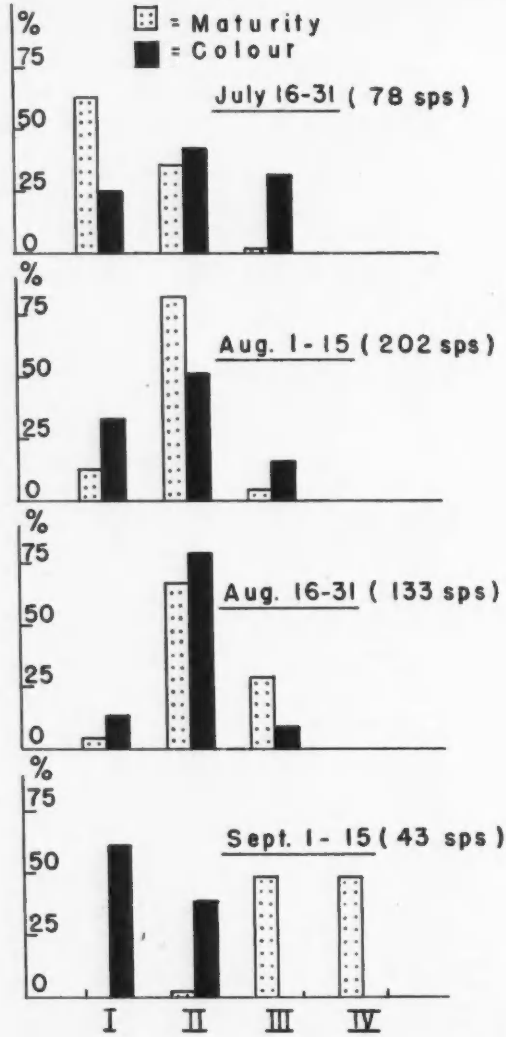

FIGURE 3.–Seasonal variation in the number of females, expressed in percentage, according to the stages of maturity and colouration of flesh, taken at the head of Grand lac Jacques Cartier, 1938.

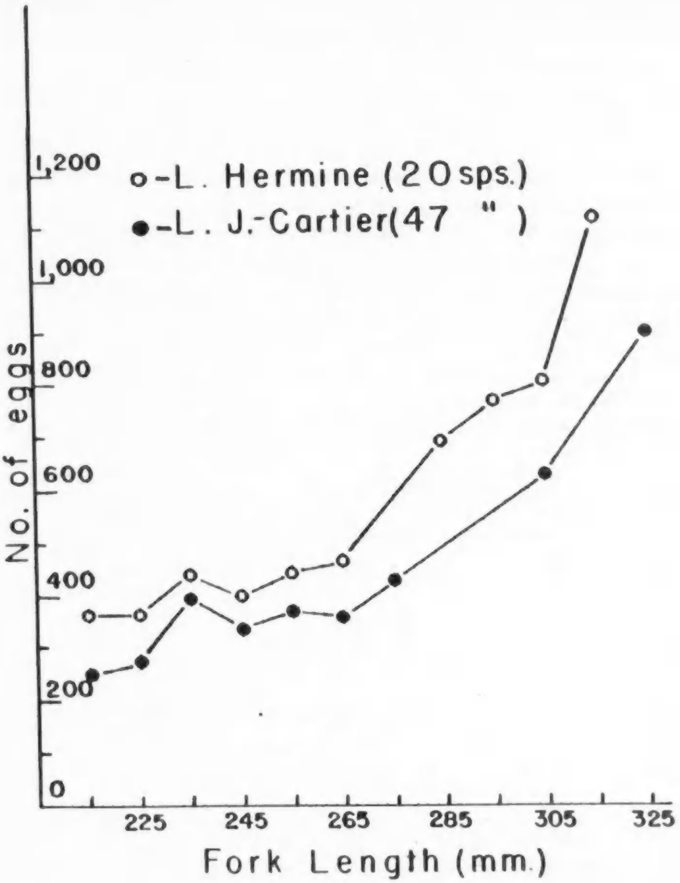

FIGURE 4.—Comparison between fecundities of females of S. *fontinalis* from two different lakes. Data in averages for mature eggs, 4 mm. in diameter.

females, 185 and 195 mm. in fork length respectively, taken on July 14. Closer to spawning time, the numbers of atretic eggs become smaller, as probably many of them have already been reabsorbed. Plates IV and V show different shapes of atretic eggs.

INTERRELATION OF DIFFERENT EGG CLASSES

To illustrate the mutual relationship between different classes of eggs, two concrete observations can be cited. In the summer of 1954, two females of S. *fontinalis* were taken. One, 6 inches (152 mm.) in length, was immature and contained only recruitment stock (Class *a*) of eggs. The other, measuring 10

inches (254 mm.), was in Stage 2 of maturity. In its ovaries, in addition to recruitment stock (Class *a*), more than 500 maturing eggs (Class *b*), 2 mm. in diameter, were found. Among the latter ova, about 90 atretic eggs (Class *c*) were seen also. These maturing and atretic eggs observed in 1954 were developed from the recruitment stock (Class *a*) present in the ovaries in 1953. The recruitment eggs of 1954 would develop into maturing eggs (Class *b*) during 1955, if our female should spawn during that year. However, not all adult S. *fontinalis* spawn regularly each year (Table XII).

A general idea of the relative numbers of the various classes of eggs may be seen in Table X and Figure 2. The six specimens shown were all taken in Grand lac à l'Epaule in 1949. Plate VI also gives an indication of the relative numbers and sizes of eggs of these classes in dissected ovaries.

TABLE XII.—Relationship between ripe and immature specimens of *S. fontinalis*, taken during the spawning season, September 18–October 3, 1952, in Lake Grelon.

FL Range (*mm.*)	Number of females			Number of males		
	Ripe	Immature	Total	Ripe	Immature	Total
150–9	2	11	13	—	12	12
160–9	1	8	9	—	7	7
170–9	4	9	13	1	6	7
180–9	3	6	9	—	7	7
190–9	2	1	3	—	6	6
200–9	1	—	1	—	7	7
210–9	—	—	—	1	—	1
220–9	1	—	1	—	6	6
230–9	3	—	3	2	2	4
240–9	—	—	—	—	1	1
250–9	—	—	—	—	—	—
260–9	1	—	1	—	2	2
270–9	—	—	—	1	—	1
Grand total	18	35	53	5	56	61
Percentage	34.0	66.0	100.0	8.2	91.8	100.0

TABLE XIII.—Degree of infection with plerocercoid cysts of ***Diphyllobothrium*** in adult sized females of *S. fontinalis* from Lake Grelon, September 18 and 25, 1952.

FL (*mm.*)	Spawning fish		Immature fish	
	Cysts		Cysts	
	Absent	Present	Absent	Present
150–9	1	—	3	6
160–9	1	—	2	4
170–9	1	2*	2	4
180–9	3	—	2	2
Total	6	2	9	16

*A single cyst was present in each fish.

Diameter of Ripe Eggs

In the experience of fish culturists (Davis, 1953, p. 32) the mature ova of speckled trout are about ⅙ inch (4.2 mm.) in diameter. Ricker (1932, p. 104) speaking about wild S. *fontinalis* in Ontario, states that "the size of eggs when spawned also varies considerably, from 3.5–5.0 mm. in diameter, the larger eggs coming from the larger trout."

In our material, a female in spawning condition, 141 mm. long, from Grand lac à l'Epaule (1939) contained the smallest ripe eggs, 3.8 mm. in diameter. However, in larger fish from different lakes, egg diameters exceeded this figure considerably. The common size of mature eggs, ready to be shed, varies from 4.0 to 4.6 mm. The largest mature ova were found in a female from Lake Metascouillac (1938), 265 mm. long, the egg being 4.8 mm. in diameter. Other details on the size of ripe ova are given in Table XV. It should be noted, however, that eggs with diameters smaller than 4 mm. probably are not completely mature.

Table XIV.—Number of *Diphyllobothrium* cysts in affected females of *S. fontinalis* from Lake Grelon, September 18 and 25, 1952.

FL (*mm.*)	*N*	Number of cysts									
		1–5	6–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	Average
150–9	6	2	2	—	1	—	—	1	—	—	16.2
160–9	4	—	—	1	1	—	1	—	1	—	38.3
170–9	6	4	—	1	—	—	—	—	—	1	15.0
180–9	2	1	—	—	—	1	—	—	—	—	19.0
Total	18	7	2	2	2	1	1	1	1	1	21.0

Table XV.—The relationship between the number of mature eggs per fish and fork lengths for 163 females of *S. fontinalis*.

Fork length (*mm.*)	*N*	Diameter of eggs (*mm.*)		Number of eggs	
		Mean	Range	Mean	Range
140–9	4	3.52	3.20–3.78	109	101–116
150–9	2	4.10	4.08–4.12	99	88–117
160–9	12	3.41	3.00–3.93	161	130–193
170–9	8	4.15	4.00–4.48	160	108–208
180–9	5	4.20	4.03–4.38	175	136–211
190–9	5	4.19	4.02–4.65	193	112–222
200–9	8	4.16	4.00–4.38	236	154–308
210–9	18	4.22	4.00–4.65	271	146–424
220–9	23	4.27	4.00–4.78	289	195–417
230–9	17	4.20	4.00–4.58	390	294–588
240–9	19	4.32	4.03–4.70	356	239–453
250–9	11	4.31	4.00–4.68	402	236–570
260–9	7	4.35	4.08–4.80	412	318–571
270–9	3	4.16	4.00–4.37	426	402–455
280–99	3	4.21	4.10–4.35	678	581–763
300–19	8	4.28	4.00–4.65	959	632–1,349
320–39	1	4.40	—	900	—
340–59	3	3.52	3.35–3.74	1,435	975–1,666
360–79	1	3.98	—	1,556	—
380–99	2	4.17	4.16–4.17	1,763	1,585–1,941
420–39	1	3.34	—	1,850	—
440–59	1	4.60	—	2,444	—
540–59	1	3.25	—	4,765	—

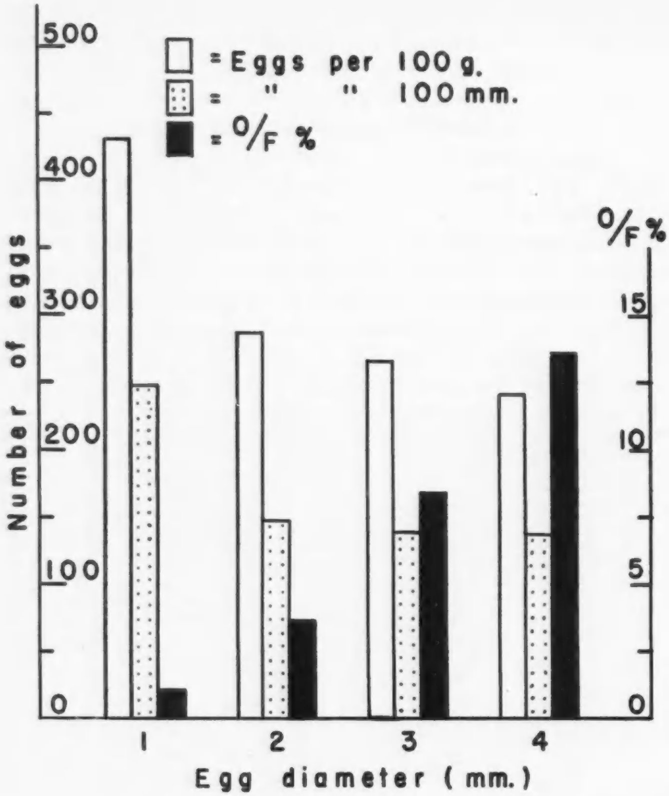

FIGURE 5.—Comparison of number of maturing eggs per 100 g. of fish weight, and per 100 mm. of fish length, as well as of maturity index; arranged according to the diameter. Data in averages, for the same 343 fish as mentioned in Tables IV–VII.

The diameter of fertilized ova apparently remains the same throughout the incubation period, as the size of the eyed eggs suggests. Thus in two samples of eyed eggs, preserved in formalin, we found the following diameters: 4 mm. for hatchery raised fish from New Hampshire, and 4.4 mm. for wild trout from Grand lac Jacques Cartier, P.Q. (Vladykov, 1954, p. 904).

RANGE IN NUMBER OF MATURE EGGS

In our material, the extreme variation in the size of the female trout, which would have spawned during the year of collection, ranged from 4½ to 22 inches (114–559 mm.). The smallest fish, which was taken in Lake du Portage on

August 16, 1938, was 115 mm. long and contained 95 eggs[13] of slightly less than 2 mm. in diameter. It is quite probable that this fish would have spawned later in the fall of the year of collection. The next larger fish, 138 mm. long, containing 143 eggs of 3.5 mm. in diameter, was taken in the Montmorency River on August 24, 1938. The largest fish, 553 mm. in length, which contained 4,765 eggs of 3.3 mm. in diameter, was caught outside the Laurentide Park, namely in Lake Wayagamack on August 8, 1940.

Stages of Maturity

As soon as *S. fontinalis* of either sex attains sexual maturity, it can spawn several years in succession. A female deposits eggs once a year during the fall or winter months according to locality. Between the two nearest reproductive seasons, there are several cyclic changes observed in its ovaries. The present author is inclined to recognize *seven* more or less distinct, *stages of maturity*[14]. In females of *S. fontinalis* these stages are characterized by the size of the ovaries, their external appearance and the diameter of the eggs. (Plates I–III and VII). In the case of Stages 1 to 5, the diameter of ova refers to the *maturing eggs* (Class *b*), while in Stages 0 and 6, to that of *recruitment stock* (Class *a*).

Stage 0: *Juvenile, immature condition*. Ovaries are very small and narrow. Eggs minute, their diameter smaller than 1 mm.

Stage 1: *Resting period*. Ovaries small, narrow, elongated, yellowish, more or less triangular, and rather hard. Egg diameter is around 1 mm. (Plate I).

Stage 2: *Early development*. General characters nearly similar to *Stage 1*, but the ovaries are larger and eggs more developed. Egg diameter is around 2 mm.

Stage 3: *Active period*. Ovaries occupy approximately half of the body cavity. Blood vessels are easily visible on the surface of the ovaries, having the appearance of a reddish network. Egg diameter is 2–3 mm.

Stage 4: *Penultimate period of ripeness*. Expanded ovaries occupy nearly all of the body cavity, and their blood vessels are now practically invisible. Eggs are nearly ripe; on pressing the abdomen, they can be made to drop out of the genital pore by clumps of threes and fours. Egg diameter is 3.5–4 mm.

Stage 5: *Spawning period*. Greatly extended ovaries, appearing as very thin sacs bulging with ripe eggs, occupy all of the body cavity. On pressing slightly the abdomen, ova can be ejected in spurts. The eggs of wild trout are usually bright orange (Plate II), but those of hatchery fish are much lighter, often even colourless. Egg diameter is 4–4.8 mm.

[13]In the case of this and the two following specimens, the numbers of eggs were counted directly, not evaluated. This was the smallest *counted* number of eggs, although several specimens had lower *evaluated* numbers.

[14]The present paper deals with the problems of fecundity of the female sex only. Therefore we omit to mention males. However in the case of the male sex identical stages of maturity can be distinguished. The definition of these stages for both males and females, in the case of haddock, was given in a previous paper (Homans and Vladykov, 1954).

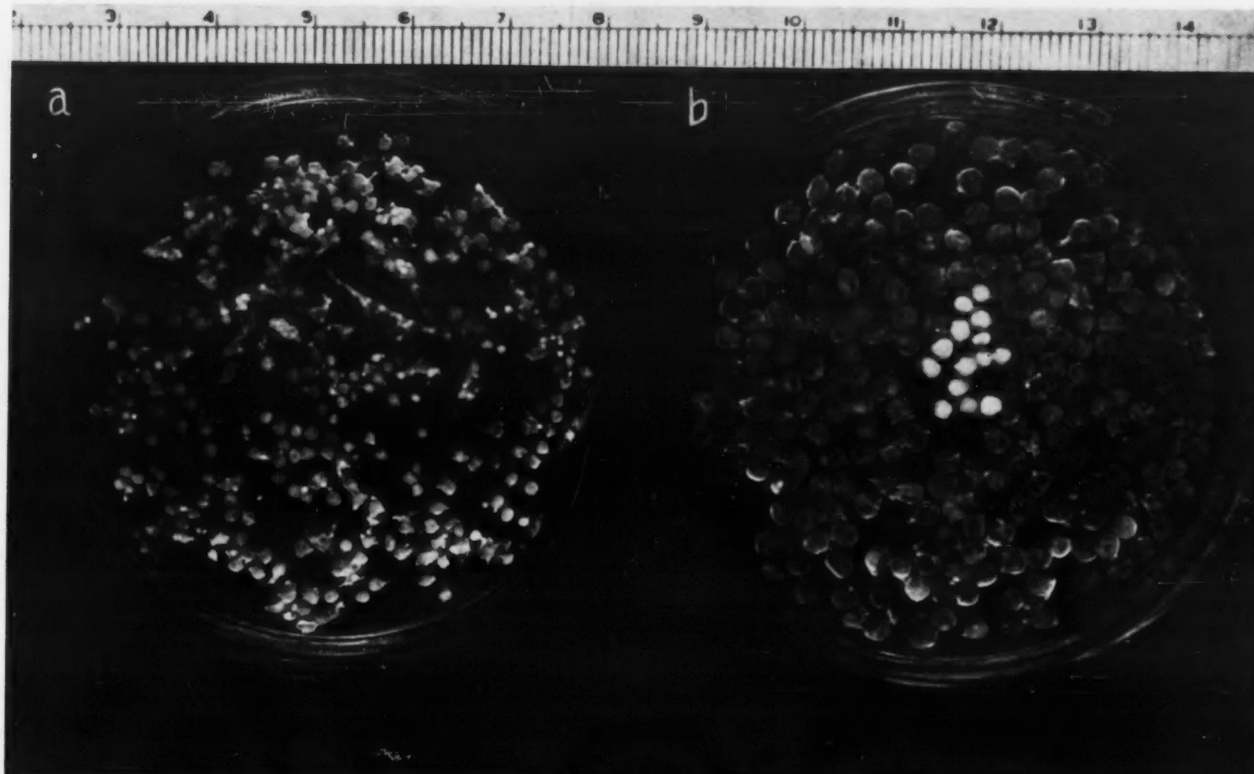

Plate VI.—Eggs from dissected ovaries from two females of S. *fontinalis* taken in Grand lac à l'Epaule in 1949. Fish *a*, 169 mm., taken on July 14th, contained 318 maturing eggs (Class *b*), 1.6 mm. in diameter; fish *b*, 174 mm., taken on August 18th, contained 257 eggs, 2.6 mm. In the centre of the right hand dish are placed 14 atretic eggs, whitish in colour. The inside diameter of the dishes is equal to 58 mm.

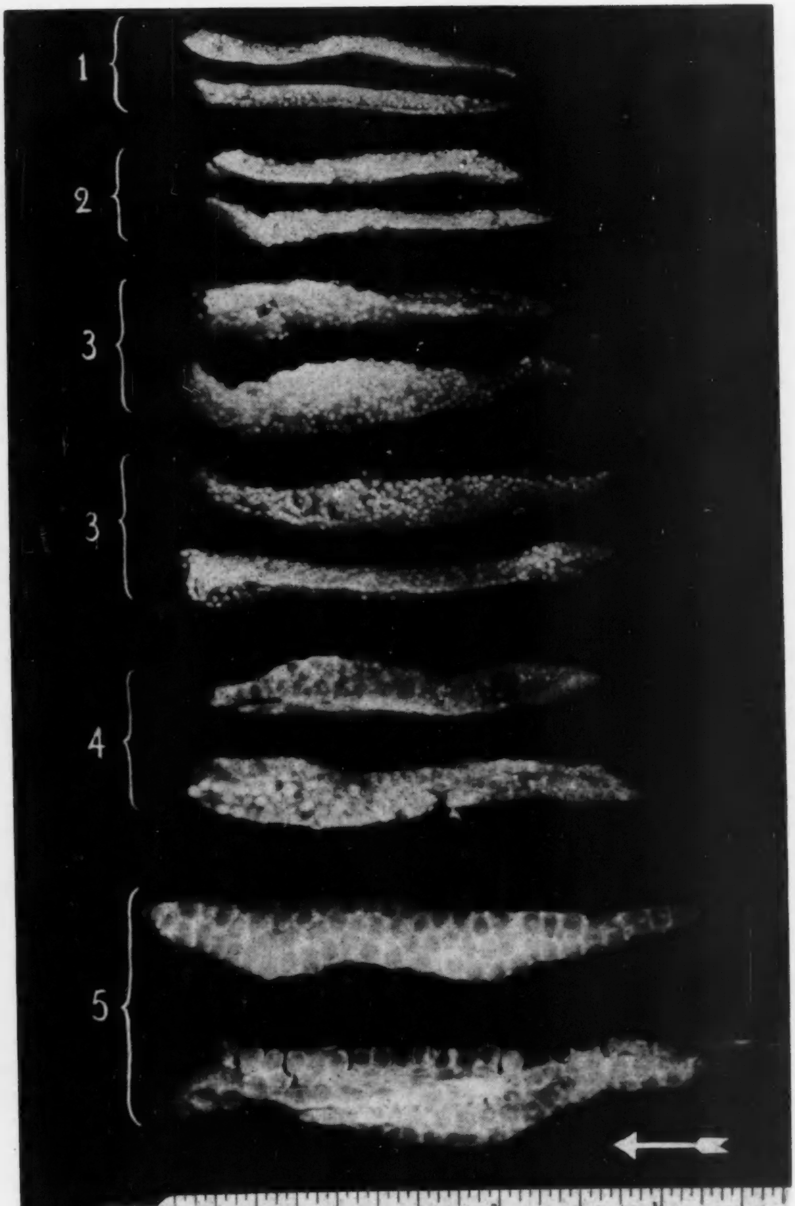

PLATE VII.—Six pairs of ovaries removed from females of S. *fontinalis*, in different stages of maturity, from 1 to 5.

Stage 6: *After spawning*. Ovaries are contracted, flaccid, filled with a reddish-violet fluid (Plate III). They contain a large number of minute eggs (Class *a*), the diameter of which is somewhat smaller than that of Stage 1.

Sometimes the ovaries of the specimens studied are intermediate in development between two of the adjacent stages of maturity. In these cases, they should be classified as follows: 1–2, or 3–4, or 4–5, etc.

A certain amount of overlapping may occur within the various stages if any one criterion is considered separately, but the stages are fairly distinct if all characters are used.

For sake of brevity (Fig. 6) the detailed (7-digit) system of stages of maturity can be condensed into four stages, designated by roman numerals, as follows:

Stage	*7-digit system*
I	comprises Stages 0 and 1;
II	„ „ 2 and 3;
III	„ „ 4 and 5;
IV	corresponds to Stage 6.

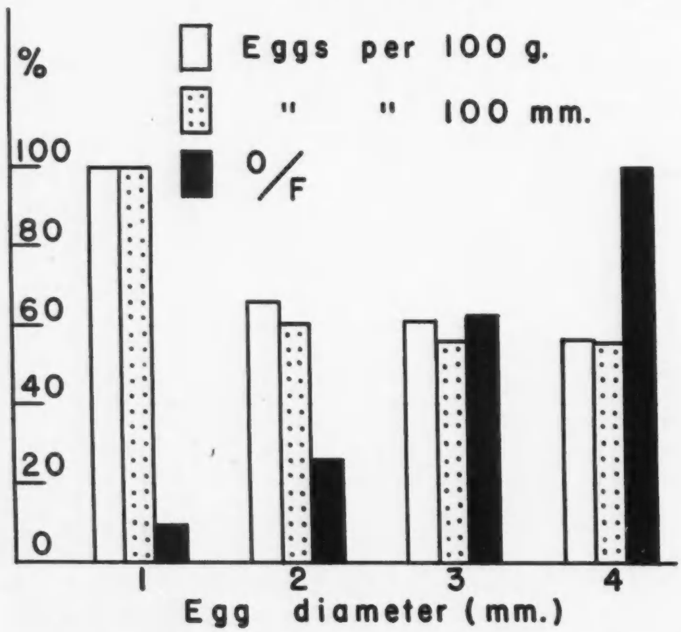

FIGURE 6.—Reduction in the number of maturing eggs per 100 g. of fish weight and 100 mm. of fish length, as well as the variation in the maturity index. Data in averages, arranged according to the egg diameter, are for the same 343 fish as mentioned in Table VIII. The number of eggs 1 mm. in diameter and the maturity index of ripe fish are considered as equal to 100.

Trout of either sex, after completing spawning in the fall, gradually pass from Stage 6 of maturity to Stage 1. If the same female is going to spawn again the next autumn, its ovaries undergo the same cycle of maturity: passing progressively from Stage 1 in the spring to Stage 6 after spawning in the fall. If, however, a spent fish (Stage 6) is not going to spawn the following autumn, its gonads remain inactive for the whole year, and thus the fish will be in Stage 1 maturity for that year also.

Frequency of Spawning

Our material shows that specimens of S. *fontinalis* of either sex can remain from one to several years in Stages 0 or 1. As soon as an individual attains Stage 2 of maturity, it will definitely spawn the same autumn. Usually trout of either sex can spawn upon reaching 130 mm. or 140 mm. in fork length. However, in certain lakes (Table XII) many trout of even larger sizes do not spawn regularly each year. Although the exact causes of this are not well understood as yet, two plausible explanations can be offered: parasites or inadequate diet.

In some cases (Tables XIII–XIV) apparently the infection by a *Diphyllobothrium* cestode[15], the cysts of which are present along the outside wall of the upper sections of the alimentary canal, retards maturation of the trout[16]. In Lake Grelon, during the spawning season, it is rather surprising to catch many trout of both sexes and of adult size, the gonads of which are in immature condition. Many of these immature fish are infested with *Diphyllobothrium* plerocercoids. In extreme cases, in each of three females we counted 52, 67 and 73 cysts respectively. Other details are given in Table XIV.

Among adult trout collected in Lake Grelon in fall of 1952, which were in immature condition, some females still retained odd large ova in the abdominal cavity, left over from the 1951 season. Most probably these specimens had not been infected by *Diphyllobothrium* the year before.

In the experience of fish culturists, only fast-growing and well-fed trout can spawn regularly. No doubt, the same requirements exist in nature. Deficiency in diet of wild stock is caused often by overcrowding. In many lakes of the Laurentide Park, due to extensive and favourable spawning beds, great numbers of small-sized trout are found.

Colour of Flesh

During maturation, not only the skin of the fish changes in colour but also its flesh. The outside and inside colouring apparently is caused by accumulation of certain carotinoid substances. The external red pigments depend rather on sexual dimorphism, the livery of the male being more brilliant than that of the female (Vladykov, 1953 & 1954). The outside colouring most often does not

[15]The identification of the plerocercoid stage of *Diphyllobothrium* worm was kindly made by Dr. Thomas W. M. Cameron and Miss B. J. Myers, Institute of Parasitology, Macdonald College, P.Q. Choquette (1948) reported the presence of this parasite in S. *fontinalis* from certain lakes in the Laurentide Park.

[16]In Europe, Hickey and Harris (1947) reported severe mortality of trout (*Salmo trutta*), in captivity, due to mass infection by plerocercoids of *Diphyllobothrium*.

correspond at all to the tint of the flesh. The condition of the flesh can be easily judged by its colour.

During the present investigation a 6-digit system was devised to characterize the colour of the flesh in the trout. Sometimes, especially when available material is not very extensive, the detailed (6-digit) system can be advantageously replaced by an abbreviated one, designated by roman numerals: I–III.

Using the nearest tints under their respective numbers as in the universal code of colours by Séguy (1936) as a base, the different colours of the flesh of speckled trout are defined as follows:

Stage	*6-digit system*
I	0–flesh greyish, approaching No. 680; 1–flesh faintly rose, No. 20;
II	2–flesh light orange rose, No. 199; 3–flesh carnation rose, No. 185;
III	4–flesh salmon colour, No. 198; and 5–flesh vermillion, No. 152.

To determine the colour of flesh, an incision is made on a side of the fish halfway down from the lateral line. Sometimes it is necessary to wipe the exposed edge free of blood.

There are in the Laurentide Park some areas, such as upper sections of the Pikauba River, where any month of the year the flesh of speckled trout is very poorly coloured, being in Stages 0 or 1. On the other hand, in other localities, such as Grand lac Jacques Cartier, local trout have highly coloured flesh (Stages 3 to 5). Moreover, the flesh of fingerlings is typically less coloured than that of adult fish.

In any particular lake, from May to October, there are regular changes in the colour of flesh of trout of both sexes. Early in spring (May–June) the colour of flesh is less pronounced, being mostly in Stage 2. During the active ripening of the fish throughout the summer (July–August), the flesh is at its best, being in Stages 3 to 5. During spawning and at least a month after, the colour of flesh fades considerably, the majority of specimens being again in Stage 2. Figure 3 illustrates the seasonal changes in the colour of flesh in connection with changes in the ripening cycle of trout.

The colour plates illustrate accurately the changes in the colour of flesh of female trout according to the stages of maturity. Fish approaching spawning (Plate II) have flesh of a much brighter hue and better tasting than young or spent individuals.

Ovarian Cycle

To recapitulate the data presented in this chapter, we must briefly state the seasonal changes in the ovaries of a mature female trout. Among wild fish in Qubec lakes, sexual maturity of females usually arrives at the age of 3 or 4 years. Among hatchery raised trout many fish of both sexes can spawn at a

precocious age of 12–18 months. Thus, at least in some cases, the whole ripening cycle of female S. *fontinalis*, from the moment of hatching to first spawning takes only 12 months. At the other extreme, a fish may be 5 or 6 years old and still be immature.

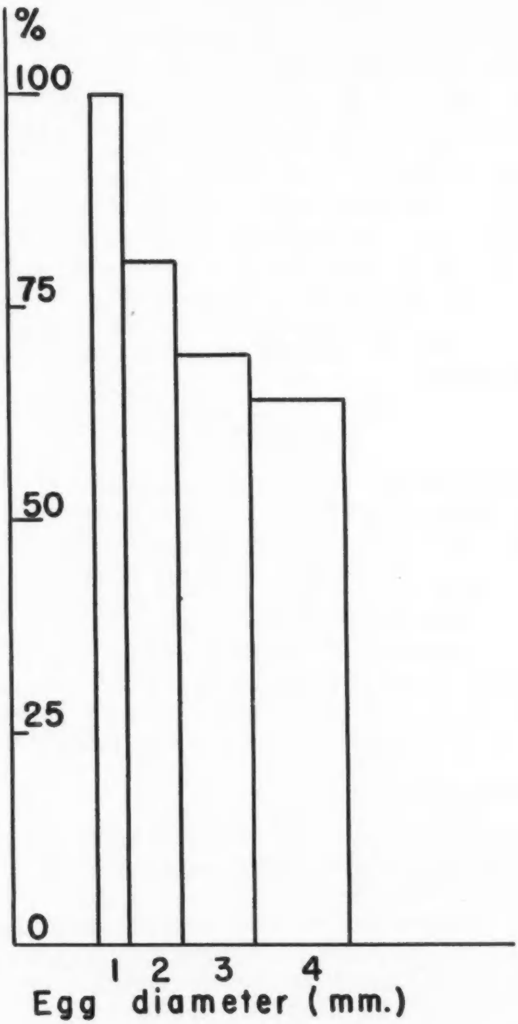

FIGURE 7.—Reduction in the number of eggs per 100 g. of fish weight during maturation. The data, in averages, are for the same 661 females as mentioned in Table II. The number of eggs 1 mm. in diameter is considered as equal to 100.

In natural conditions, a typical transition from immaturity (Stage 0) to spawning (Stage 5) requires nearly two years, as mature ova need almost two years to develop from recruitment eggs (less than 1 mm.) into mature eggs (at least 4 mm. in diameter). During the first year of ripening the recruitment eggs (Class *a*) increase considerably in numbers, from a few hundreds in May or June to one or several thousands in the case of large females late in the autumn (Table X), but their size remains practically the same (Fig. 2). The next spring, apparently no more eggs of current Class *a* enter into the complement of last year's maturing ova. Eggs of the present Class *b* (which the year before were in Class *a*) begin to increase in size, from less than 2 mm. in diameter in May and June to more than 4 mm. in September (Table IX). The *increase in size of maturing ova was accompanied by decrease in numbers*, through atresia. The extent of reduction of maturing ova will be discussed farther in the paper (Figs. 5–7).

In conclusion it can be stated, that the ovarian ripening cycle in S. *fontinalis* does not depend to any great extent on the age or size of the fish, but mainly on the amount of food assimilated previous to spawning. Better feeding conditions (in hatchery or in a lake), the earlier in age maturity arrives and the more eggs produced by the female.

FECUNDITY

One must distinguish at the beginning between the term "fecundity" and the number of eggs contained in a fish at any given moment. The real fecundity should be defined as "fruitfulness or the ability to produce large numbers of progeny". The term may therefore only be applied to speckled trout with reference to the quantity of mature eggs produced in spawning. It should be noted, however, that *the number of ripe ova* present in the ovaries previous to spawning *is the smallest* in comparison to the number of maturing eggs, which this fish had earlier in the season. As compensation for the reduction in numbers, there is a pronounced increase in the size of the mature eggs. For further generalization on the subject, the reader is referred to an interesting paper by Svärdson (1949).

Types of Fecundity

Throughout the present paper, we shall use different methods to define the fecundity in female speckled trout, as was done for other fish species by certain authors, such as Määr (1949) or Toots (1951).

(a) *Total fecundity*. Under this term, we shall consider the *total number of ripe eggs* present in both ovaries. It is known, that *the relation between total number of eggs and fish length is a positive one,* and that every population has its own typical regression line (Tables I, II, VII; Figs. 8, 9).

(b) *Relative fecundity*. To make observations on fish of different sizes more comparable, we use the number of maturing eggs (Class *b*) found in both ovaries (1) per 100 g. of fish weight, or (2) per 100 mm. of fork length. *There exists a negative relationship between relative fecundity and the diameter of eggs* (Tables III, VIII; Figs. 5, 6).

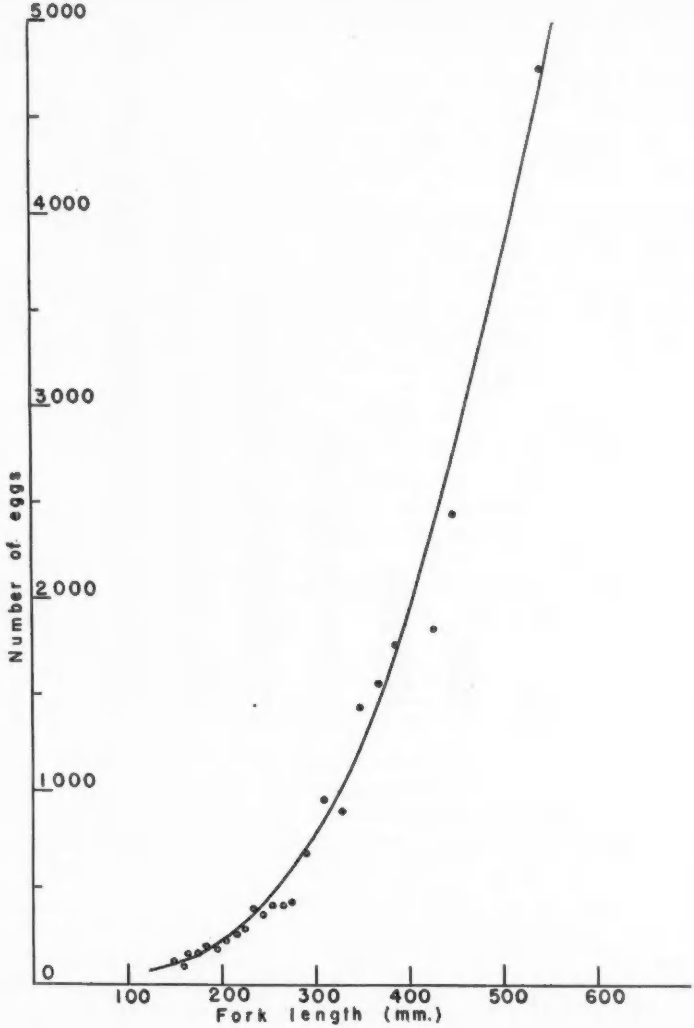

FIGURE 8.—The curvilinear relationship between the number of mature eggs per fish and fork length, for 163 females of S. *fontinalis*.

VARIATION IN NUMBER OF EGGS

Our material clearly shows, that there exists a pronounced variation in both total and relative fecundity of S. *fontinalis*. Not all the causes are well understood as yet, nevertheless certain of them can be described.

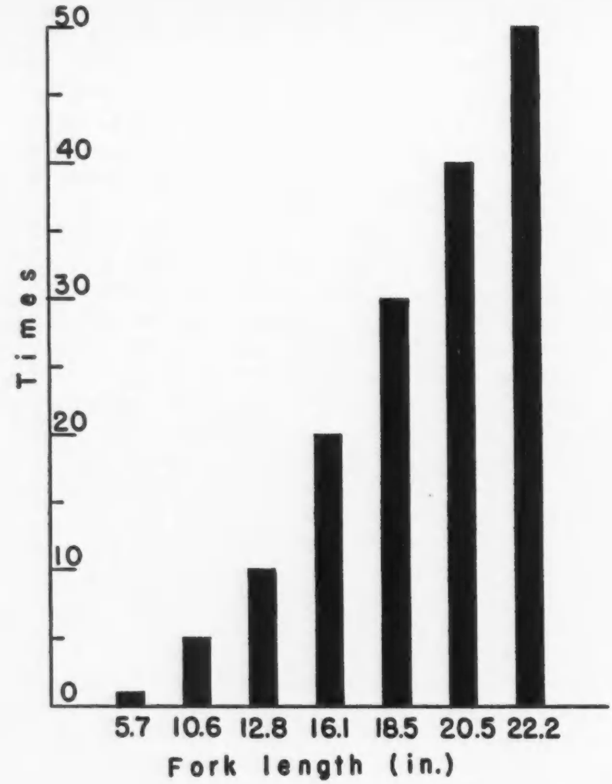

FIGURE 9.—Proportional increase in the number of ripe eggs with the size of female of *S. fontinalis*. Data are in averages, based on Table XVI. The number of eggs of a 5.7-inch fish is equal to 100.

(a) *Individual variations*. In this respect, the speckled trout is not different from other species, as Table X shows. There are too many causes of variation in fecundity from one individual to another to mention them here. It is enough to state their existence only.

(b) *Variation with the season*. If the number of developing eggs (Class *b*) is counted from a group of fish of the same size (and presumably of corresponding age), taken from the same lake over the developmental season, it will be found that the number of eggs is higher at the beginning of the season than later. As the diameter of the eggs increases, there is a drop in the number of maturing eggs (Tables I, VI; Fig. 1). Thus the variation with the season is rather the variation with the egg diameter.

(c) *Variation with size of fish.* There exists in all fish species a direct relation between the length of females and the number of eggs. Our material shows also a definite increase in egg productivity in practically all diameter groups with increase in size of fish (Tables I, II, VI, XVI; Fig. 1). The relation between the number of eggs and length of female was considered by several authors, as Ricker (1932), Vladykov and Legendre (1940), and Smith (1947), as curvilinear. However, Allen (1956) for 14 fish from a Wyoming beaver pond prefers to express it as a rectilinear relation.

(d) *Variation with habitat.* Specimens from different lakes show a distinct variation in the numbers of eggs. There are lakes with a high productivity (Hermine, Long, etc.), and those (Grand lac à l'Epaule, Grand lac Jacques Cartier, etc.) where fish carry only small numbers of eggs. Other details are found in Tables V–VII, and Figure 4. It is important to note that conditions prevailing in a certain lake can be changed, with the consequence that the fecundity of local speckled trout is changed also. Using Grand lac à l'Epaule[17] as an example (Table VI) we can see that fish in 1949 produced many more eggs than in the 1938–39 period. In 1949, the local beaver colony had built a high dam in an important spawning brook, resulting in relatively small production of wild trout fingerlings. This lake formerly was overstocked with small fish due to excessive spawning beds. No doubt, the higher fecundity in 1949 resulted from more abundant food available for adult trout.

It should be noted that S. *fontinalis* from the Laurentide Park produce much lower numbers of eggs for a given length than did fish studied by Smith (1947) or Allen (1956).

(e) *Variation with heredity.* In the case of wild stock of speckled trout, it is very difficult to separate individual causes of variations in fecundity. Some of them can probably depend on heredity, but others, most frequent, are caused by variations in the abundance and availability of food.

On the other hand, it is a common practice among fish culturists to raise hatchery-reared stock, which was selectively bred for high egg yields. Hatchery fish of certain strains can produce at their first spawning about four times as many eggs as in the wild state. In spite of the fact of this very high fecundity, it is not very clear whether *the high egg yield* of hatchery trout *is actually hereditary in itself*. Hayford and Embody (1930, p. 109), summarizing their experiments on selective breeding, said:

"1. Continued increase in the rate of growth resulting in larger fingerlings and breeders.

"2. Marked increase in the average number of eggs produced by each female at the first and second spawnings."

In a more recent paper, Hayford (1932, p. 126) gives additional details of how to proceed in selecting fish for high egg yields. He states: "As soon as the young trout attain a size of two to four inches, we run them through the sorting boxes and keep only the three- and four-inch fish. The two-inch trout that are

[17]A description of physico-chemical conditions of this lake is given by Vladykov (1942).

the runts are immediately planted. By getting rid of the runts and rearing only the more rapidly growing fish we utilize the food more efficiently."

Thus his method, like that of other culturists, consists in *keeping for breeding only fast growing individuals.* So the heredity in this case affects primarily the ability of a trout to better utilize the food and consequently to produce more eggs. Or in other terms, *better feeding prevents excessive atresia of maturing ova.*

Reduction in Numbers of Eggs

No direct observations are available as to the fact of the reduction of eggs (Class *b*) during maturation of individual females of S. *fontinalis* due to atresia, however, considerable indirect proofs (Tables I, II, VI, IX; Figs. 1, 5) suggested this possibility. How otherwise can a female survive, when the volume of its maturing eggs increases many fold. In fact, a volume of an egg 1 mm. in diameter is equal to 0.52 $mm.^3$ and those of an egg 4 mm. and 4.5 mm. in diameter are 33.5 and 47.7 $mm.^3$ respectively. If all eggs reached maturity the fish's body would burst!

In order to have an approximate idea of the extent of reduction through atresia, we can consider the number of maturing eggs (Class *b*) 1 mm. in diameter as equal to 100, and we shall compare it with the numbers of ova of larger diameters (Table IX). This method we can call *reduction in the total fecundity.* To establish the magnitude of *reduction in the relative fecundity,* we shall use as a base the number of eggs 1 mm. in diameter per 100 g. of fish weight or 100 mm. of fish length (Tables III, VIII, IX; Figs. 5, 6). Although there exist small differences between the results presented in Tables III, VIII and IX, they probably depend to a certain extent on numerical inequality of samples. Nevertheless we can quite safely consider that only 56–61% of maturing eggs (Class *b*) eventually ripen. This reduction of nearly half of the maturing eggs occurs during 3 or 4 summer months. If we take into consideration also the number of eggs of recruitment stock (Class *a*), then the total reduction in both Classes *a* and *b* due to atresia will amount to nearly 80% (Table X).

Previous authors apparently did not pay much attention to the importance of the diameters of eggs, as they lumped together all females regardless of the size of their eggs.

Ovary Weight

Another way to comprehend the fecundity of fish is to follow the changes in the weight of ovaries due to egg ripening. This approach, already used by us for lampreys (Vladykov, 1951), is applicable for trout as well.

The weight of both ovaries in grams was expressed in percentage of the total weight in grams of a female and was called *maturity index.* Thus the higher the index, the higher is the degree of maturity (Fig. 5).

Tables V and VIII contain pertinent data. In our material, the average maturity index varies from 1.2% when the egg diameter is equal to 1 mm., to 13.6% in the case of ripe eggs of 4 mm. Considering the index for ripe ovaries as

equal to 100, relative indices for less developed ovaries will be as follows: 62.5, 26.6 and 8.5 (Table VIII). It should be noted that in the case of eggs 3 mm. in diameter, their number per 100 g. of fish weight or 100 mm. of fish length expressed in percentage, as well as their maturity index, will be practically identical, namely 62, 57, and 63 respectively (Table VIII, Fig. 6).

NUMBER OF EGGS SPAWNED

In the preceding section, several facts were presented to show that a definite reduction in the number of eggs takes place during their maturation. This numerical reduction is manifest in both relative and total fecundities. On basis of the above data and by close examination of Tables II and VI, one can see that the extent of the reduction of the number of mature ova is particularly pronounced among eggs of smaller diameters (1 or 2 mm.). As soon as maturing ova attain a diameter greater than 3.5 mm., their numbers remain practically unchanged. If atresia continues, however, the reduction in egg numbers is very slight. Thus if we need to compare fecundities of speckled trout from different localities, we must select fish completely mature (with egg diameters 4.0–4.8 mm.), or, at least, those with eggs not smaller than 3.5 mm. in diameter.

Table XV and Figure 8 contain information on the number of mature ova spawned by wild speckled trout in the Laurentide Park. In all, 163 fish with fork lengths varying from 140 to 553 mm. were selected. Among these only 6 females contained eggs somewhat smaller than 4 mm. in diameter. These eggs are not fully mature, but due to their large size it is very unlikely that their number would be further reduced to any considerable extent by atresia.

The average number of eggs spawned varied from 90 to nearly 4,800, according to the size of the female. The shape of our curve is very similar to that for Ontario fish mentioned by Ricker (1932). Considering a female of 144 mm. (or 5.7 inches), probably spawning for the first time and shedding on the average 100 eggs, as a base, we compare it with larger specimens (Table XVI). The size

TABLE XVI.—Proportional increase in the number of ripe eggs with the size of female of *S. fontinalis*. Data in averages, based on Table XV.

Fork length		Number of eggs	Increase (times)
mm.	*inches*		
144	5.7	100	1
190	7.5	200	2
215	8.3	300	3
240	9.4	400	4
270	10.6	500	5
325	12.8	1000	10
375	14.8	1500	15
410	16.1	2000	20
440	17.3	2500	25
470	18.5	3000	30
490	19.3	3500	35
520	20.5	4000	40
540	21.3	4500	45
565	22.2	5000	50

TABLE XVII.—Relation between the diameter of eggs and the number of eggs per gram of ovaries weight. Data, in averages for 343 females, are for the same specimens as those mentioned in Tables IV–VII.

Lake	Diameter of eggs in mm.															
	1.00–1.49		1.50–1.99		2.00–2.49		2.50–2.99		3.00–3.49		3.50–3.99		4.00–4.49		4.50–4.99	
	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs	Ave. Di.	Eggs
	mm.	*No.*	*mm.*	*No.*	*mm.*	*No.*	*mm.*	*No.*	*mm.*	*No.*	*mm.*	*No.*	*mm.*	*No.*	*mm.*	*No.*
G.L. à l'Epaule (1938–39)	—	—	—	—	2.19	124	—	—	3.15	43	3.83	25	4.18	20	—	—
G.L. à l'Epaule (1949)	1.40	531	1.79	276	2.40	95	2.65	73	3.16	43	3.77	26	4.21	19	4.65	16
Long	—	—	—	—	2.34	112	2.83	61	3.30	39	3.72	27	4.19	19	4.54	15
G.L. J.-Cartier (Head)	—	—	1.94	185	2.47	93	2.80	62	3.24	38	3.72	25	4.21	19	4.64	14
G.L. J.-Cartier (3rd Rapid)	—	—	—	—	—	—	—	—	3.42	34	3.79	26	4.20	19	4.56	18
Hermine	1.34	539	1.72	289	2.29	129	2.78	66	3.27	41	3.75	26	4.21	18	—	—
Jupiter	—	—	—	—	2.20	124	2.68	63	3.21	41	3.70	29	4.10	16	—	—
Grelon	—	—	—	—	—	—	—	—	3.10	44	3.60	29	4.10	19	4.80	16
Total	1.39	537	1.77	269	2.25	118	2.73	64	3.24	40	3.73	26	4.19	19	4.63	15

of fish which lay 5, 10, 15, 20 etc. times more eggs would be 270, 325, 375, 410 mm. etc. respectively. Other details are given in Table XVI and Figure 9.

The knowledge of the number of eggs spawned by fish of different sizes is of prime importance in fish management. It would be more economical from a point of view of food consumption to keep in a lake for reproductive purposes

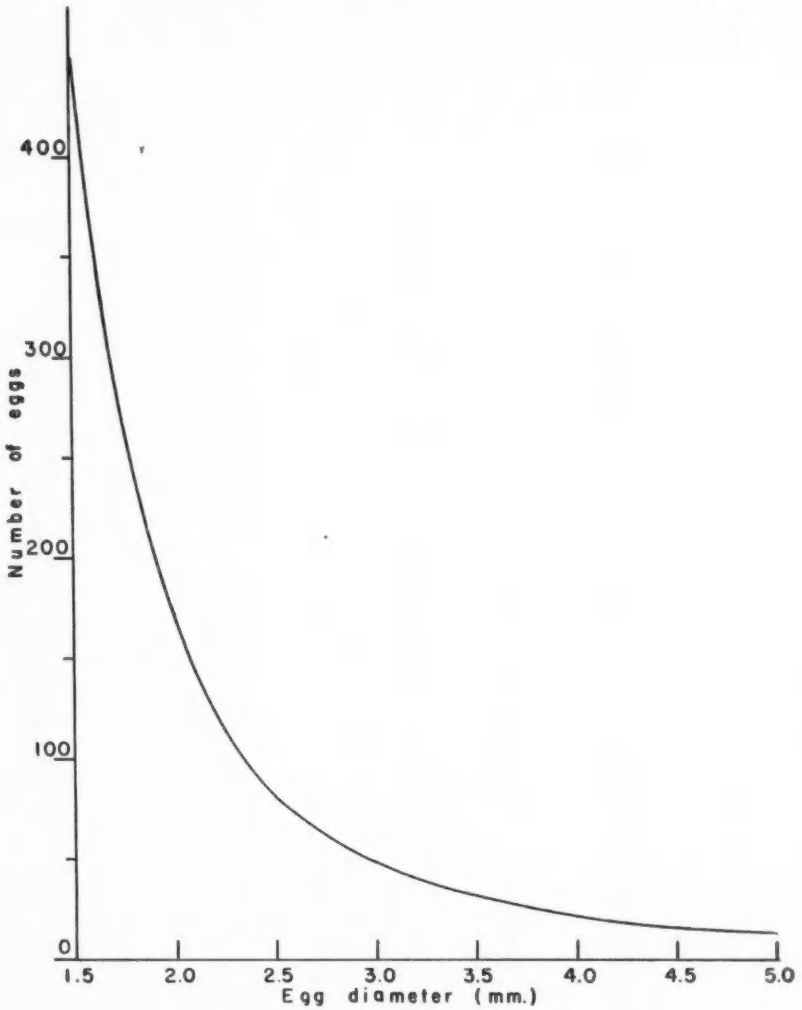

FIGURE 10.—The relationship between the diameter of eggs of *S. fontinalis* and their number per gram of ovaries. Data based on the same 343 females as mentioned in Table XVII.

1000 females, 11–13 inches, instead of 5,000 fish, 6–8 inches long, which would lay the same number of eggs.

METHOD OF NUMERICAL ESTIMATION OF TROUT EGGS

In our earlier work (Vladykov and Legendre, 1940) we evaluated the number of eggs present in the ovaries by the volumetric method. During the

TABLE XVIII.—The relationship between the egg diameter and the number of eggs per gram of ovaries in females of *S. fontinalis*.

Diameter	No. per gram	Diameter	No. per gram	Diameter	No. per gram	Diameter	No. per gram
(*mm.*)		(*mm.*)		(*mm.*)		(*mm.*)	
1.00	1,000	2.00	172	3.00	49	4.00	21.5
2	970	2	166	2	48	2	21.2
4	932	4	160	4	47	4	20.9
6	892	6	154	6	46	6	20.6
8	860	8	150	8	45	8	20.3
1.10	830	2.10	145	3.10	44.5	4.10	20.0
2	804	2	140	2	43.9	2	19.7
4	780	4	136	4	43.3	4	19.4
6	756	6	132	6	42.7	6	19.1
8	732	8	128	8	42.1	8	18.8
1.20	708	2.20	125	3.20	41.5	4.20	18.5
2	688	2	122	2	40.8	2	18.3
4	668	4	118	4	40.1	4	18.1
6	648	6	114	6	39.4	6	17.9
8	632	8	111	8	38.7	8	17.7
1.30	612	2.30	108	3.30	38.0	4.30	17.5
2	594	2	105	2	37.4	2	17.3
4	576	4	102	4	36.8	4	17.1
6	560	6	99	6	36.2	6	16.9
8	544	8	96	8	35.6	8	16.7
1.40	526	2.40	94	3.40	35.0	4.40	16.5
2	510	2	92	2	34.4	2	16.4
4	490	4	89	4	33.8	4	16.3
6	478	6	86	6	33.2	6	16.2
8	462	8	84	8	32.6	8	16.1
1.50	448	2.50	82	3.50	32.0	4.50	16.0
2	432	2	80	2	31.5	2	15.9
4	418	4	78	4	31.0	4	15.8
6	406	6	76	6	30.5	6	15.7
8	392	8	74	8	30.0	8	15.6
1.60	378	2.60	72	3.60	29.5	4.60	15.5
2	362	2	71	2	29.0	2	15.4
4	350	4	70	4	28.5	4	15.3
6	336	6	68	6	28.0	6	15.2
8	324	8	67	8	27.5	8	15.1
1.70	312	2.70	66	3.70	27.0	4.70	15.0
2	300	2	65	2	26.6	2	14.9
4	286	4	64	4	26.2	4	14.8
6	276	6	62	6	25.8	6	14.7
8	264	8	61	8	25.4	8	14.6
1.80	254	2.80	60	3.80	25.0	4.80	14.5
2	244	2	59	2	24.8	2	14.4
4	234	4	58	4	24.6	4	14.3
6	226	6	56	6	24.4	6	14.2
8	216	8	55	8	24.2	8	14.1
1.90	208	2.90	54	3.90	24.0	4.90	14.0
2	200	2	53	2	23.5	2	13.9
4	192	4	52	4	23.0	4	13.8
6	186	6	51	6	22.5	6	13.7
8	178	8	50	8	22.0	8	13.6

TABLE XIX.—Comparisons between actual and calculated egg counts in *Salvelinus fontinalis*.

Egg diam. (*mm.*)	Actual count	Calculated count	Difference %
	1.0–1.99 mm.		
1.30	720	704	−2.2
1.30	514	490	−4.7
1.35	855	824	2.5
1.43	771	775	0.5
1.46	796	809	−1.6
1.49	658	684	4.0
1.49	795	821	−3.3
1.80	361	381	5.5
1.86	491	526	7.1
1.91	496	490	−1.2
Mean	646	650	+0.7
	2.0–2.99 mm.		
2.00	226	241	6.6
2.00	262	275	5.0
2.00	169	172	1.8
2.05	139	134	−3.6
2.18	246	245	−0.4
2.20	198	202	2.0
2.28	317	325	2.5
2.35	266	263	−1.1
2.40	185	188	1.6
2.48	138	126	−8.7
Mean	215	217	+1.2
	3.0–3.99 mm.		
3.00	178	176	−1.1
3.00	251	225	−10.4
3.15	288	284	−1.4
3.20	313	303	−3.2
3.30	273	251	−8.1
3.45	247	252	2.0
3.45	329	323	−1.8
3.68	365	394	7.9
3.75	481	465	−3.3
3.95	331	322	−2.7
Mean	306	300	−2.0
	4.0–4.99 mm.		
4.05	214	201	−6.1
4.08	288	276	−4.2
4.08	1152	1118	−3.0
4.10	164	164	0
4.15	141	139	−1.4
4.20	892	900	0.9
4.23	233	212	−4.7
4.38	221	231	4.5
4.48	221	235	6.3
4.65	141	135	−4.3
Mean	367	361	−1.5

present study, we followed another method, even more accurate, which proved to be useful in the case of lampreys (Vladykov, 1951). This method is based on an observation that the weight of ovarian tissues in S. *fontinalis* is equal to a very small fraction in comparison to the weight of eggs.

After plotting on graph paper a curve, denoting the number of eggs of different diameters per gram of ovaries, a definite relation between the two components was apparent. Although we were unable as yet to find an appropriate mathematical equation to express this relation, this curve was very useful. Knowing diameters of eggs in millimeters, we can read directly from the curve (Fig. 10) the number of eggs present in one gram of the ovaries. The total number of eggs for a female was obtained by multiplying this figure by another, corresponding to the total weight of the ovaries in grams. Table XVIII contains pertinent details.

In order to check on the validity of our method, we are adding Tables XIX and XX. In the first table are compared the actual and calculated egg counts for 10 females, selected at random from each of four different egg diameter groups. The average difference between actual and calculated counts was very small, no more than 2% (Table XIX).

In Table XX all available samples were used. The differences between actual and evaluated egg numbers were arranged into five groups: 0–4, 5–9, 10–14, etc. Among 261, only 13 specimens showed a difference greater than 14%. These differences, no doubt, should be attributed to the errors made in the counting of eggs by different persons, rather than to the inaccuracy of the present method.

It would be interesting to try the above described method of evaluation of eggs in other species of Salmonidae.

TABLE XX.—Differences between numbers of eggs counted and those determined by an "egg diameter-ovary weight method" in *S. fontinalis*. Details are found in text.

Egg diameter	Differences between counted and calculated numbers											
	0–4		5–9		10–14		15–19[a]		20–27[a]		Total	
mm.	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1.00–1.99	10	35.7	5	17.9	4	14.3	3	10.7	6	21.4	28	100.0
2.00–2.99	17	38.6	17	38.6	8	18.2	—	—	2	4.6	44	100.0
3.00–3.99	71	68.9	27	26.2	5	4.9	—	—	—	—	103	100.0
4.00–4.99	58	67.5	18	20.9	8	9.3	—	—	2	2.3	86	100.0
Total	156	59.8	67	25.7	25	9.6	3	1.1	10	3.8	261	100.0

[a]The number of eggs in these 13 specimens was, no doubt, inaccurately counted, so they should be excluded from any further consideration.

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The determination of egg numbers, in chronological order, was made by the following assistants: V. Legendre, J.-P. Cuerrier, P. Lespérance, M. T. H. Brodeur, and D. P. Scott.

Mr. David P. Scott also had the task of summarizing the data up to 1951 and also made the photographs of trout ovaries. Mr. Gerard Beaulieu verified the mathematical treatment of data and prepared the graphs. Mme Germaine Bernier Boulanger most expertly executed in water colours, the three female trout in different stages of maturity.

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The authorities of the Quebec Department of Game and Fisheries provided the necessary funds.

To all these persons, the author wishes to express his gratitude.

RÉSUMÉ EN FRANÇAIS

Pour ce travail macroscopique, plus de 1,000 femelles de truites mouchetées, provenant du Parc des Laurentides dans le Québec, furent examinées. De ce nombre, 747 spécimens ont reçu une attention particulière. Dans les ovaires de truites adultes, il y a trois sortes d'œufs: *stock de base* (Classe *a*), *mûrissant* (Classe *b*), et *atrétiques* (Classe *c*). Au cours de la maturation de la femelle, le nombre d'œufs (Classe *b*) diminue par l'atrésie, mais leur diamètre devient plus grand. Pour comparer la fécondité entre diverses populations de truites, il faut choisir celles dont les œufs sont presque mûrs. Le diamètre des œufs mûrs, proches de la fraye, préservés en formol, varie de 3.8–4.8 mm. Il existe une relation directe entre le nombre des œufs mûrs et la taille du poisson: les nombres extrêmes sont 90 et 4,800 œufs, et la taille des poissons va de 6 à 22 pouces. Les truites, provenant de lacs riches en nourriture, sont plus proléfiques. Une méthode simplifiée fut établie pour déterminer le nombre d'œufs dans les ovaires. Les stades de maturité des femelles furent déterminés selon un système à 7 grades différents. La couleur de la chair fut classifiée selon un système à 6 grades différents.

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After the present article was submitted for publication, there appeared a valuable volume by I. C. Jones and P. Eckstein 1955. "The comparative endocrinology of vertebrates. Part I. The comparative physiology of reproduction and the effects of sex hormones in vertebrates." Memoirs Soc. for Endocrinology, No. 4, X, 253 pp., Cambridge, England.

In this volume appeared the two following articles: one by W. S. Hoar, "Reproduction in teleost fish" (pp. 5–24), and the other by J. M. Dodd, "The hormones of sex and reproduction and their effects in fish and lower chordates" (pp. 166–187). Both articles are interesting and contain useful bibliography.

The Biology of Arctic Char (*Salvelinus alpinus* L.) in Northern Labrador[1]

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ABSTRACT

Arctic char (*Salvelinus alpinus* L.) from the commercial sea run were sampled at five stations in northern Labrador. Otoliths were used for age determination. In the southern part of the range—Adlatok and Nain—commercial size is reached at 6 years and at places farther north in 7 years. There is also a tendency for older fish to occur as one proceeds north.

Age, weight, and length frequencies as well as their relationship to one another were determined.

Vertebral counts indicate little, if any, intermingling of populations between: Adlatok and Nain, Okkak Bay and Hebron, Adlatok and Ramah, Nain and Hebron. Fin ray counts conform with the vertebral results but indicate no significant difference between Adlatok and Nain or Nain and Okkak Bay fish.

Variations in flesh colour from white to deep red is a distinct characteristic of Arctic char in northern Labrador; flesh colour has a distinct bearing on the market value of the fish.

Principal food items included capelin, launce, young of mailed sculpin, Amphipoda, and Euphausiacea.

CONTENTS

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INTRODUCTION

In common with other areas of arctic and sub-arctic waters of eastern North America, Arctic char (*Salvelinus alpinus* L.) are abundant in Labrador waters especially in the area north of Cape Harrison; south of this point they have been frequently reported but the southern limit has not been precisely established. Arctic char taken by tourists in the Pinware River near Blanc Sablon, southern Labrador, have been seen by the authors.

The collection of data for this paper began early in July, 1953, and continued until mid-August of the same year. Arctic char of random size were purchased from fishermen at five stations, progressing northwards, as follows: Adlatok (near Hopedale), Nain, Okkak Bay, Hebron, and Ramah; the last station is about 115 miles south of Cape Chidley. The above stations are on the sea coast (Fig. 1) and are distant some 50 to 100 miles from each other.

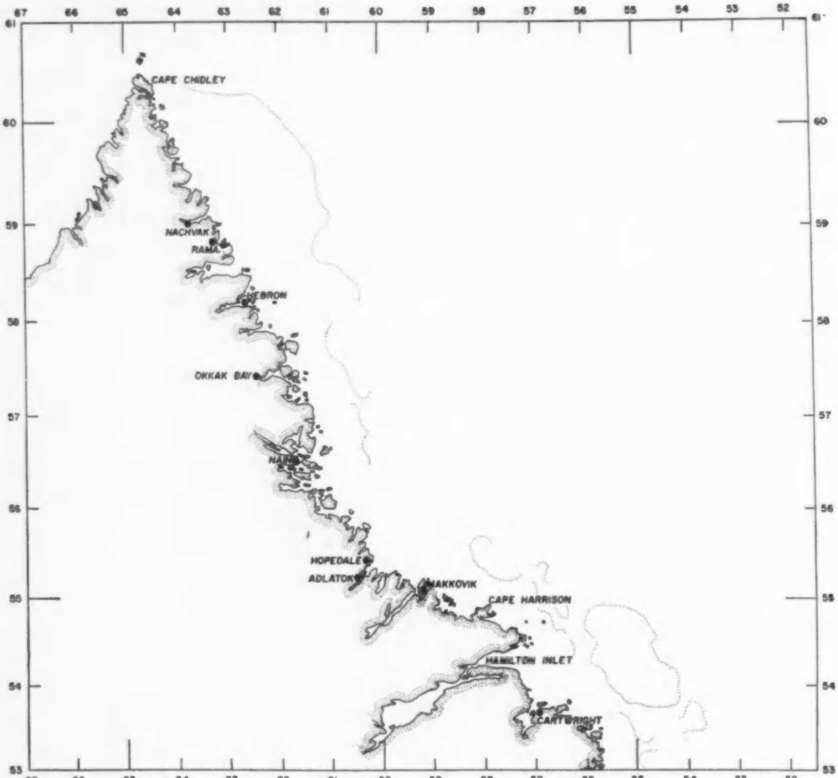

Figure 1.—Map of northern Labrador showing places mentioned in the text (Latitude North and Longitude West in degrees).

THE FISHERY

Arctic char of northern Labrador, i.e., from Hopedale north, are particularly important in the economy of the Labrador native. During the period 1944–54 inclusive, the annual production of pickled Arctic char was as shown in Table I.

TABLE I.—Arctic char marketed from the region Hopedale–Hebron. One barrel equals 220 lb.

Year	Barrels
1944	100
1945	260
1946	230
1947	635
1948	1,220
1949	450
1950	450
1951	330
1952	840
1953	1,021
1954	746
Total	6,282
Average	571

The total production, during 11 years as shown, was 6,282 barrels with an average annual production of 571 barrels, 125,602 lb. or 57,000 kg. At $30.00 per barrel the gross value was $17,130.00 per annum; the average fisherman caught from 10 to 20 barrels during the season. In the years 1944–49 and earlier, white-fleshed char (about 20% of the landings) was purchased. Since that time, however, only pink- and red-fleshed char have been marketed. Production as shown in Table I represent, therefore, Arctic char marketed rather than total landings.

The trend in production, with peaks of 1,220 and 1,021 barrels for 1948 and 1953 respectively, is not indicative of the availability of char; rather, it seems, that when the price of codfish is low with respect to char the latter are fished throughout the season. On the other hand, when the price of cod is high, the fishermen desert their char nets early in the season in favour of cod and this results in low production of char.

Sporadic catching on a commercial scale has been attempted by Newfoundland schooner fishermen. At Nachvak, 100 miles south of Cape Chidley and 15 miles north of Ramah, for example, the schooner *Patriot* with gill-nets, a crew of

TABLE II.—Annual catch of Arctic char at Nachvak by the *Patriot*, 1947–50.

Year	Catch	Crew	Nets	Average catch
	barrels			*barrels per net*
1947	300	6	12	25.0
1948	360	7	22	16.4
1949	200	7	24	8.3
1950	50	6	24	2.1

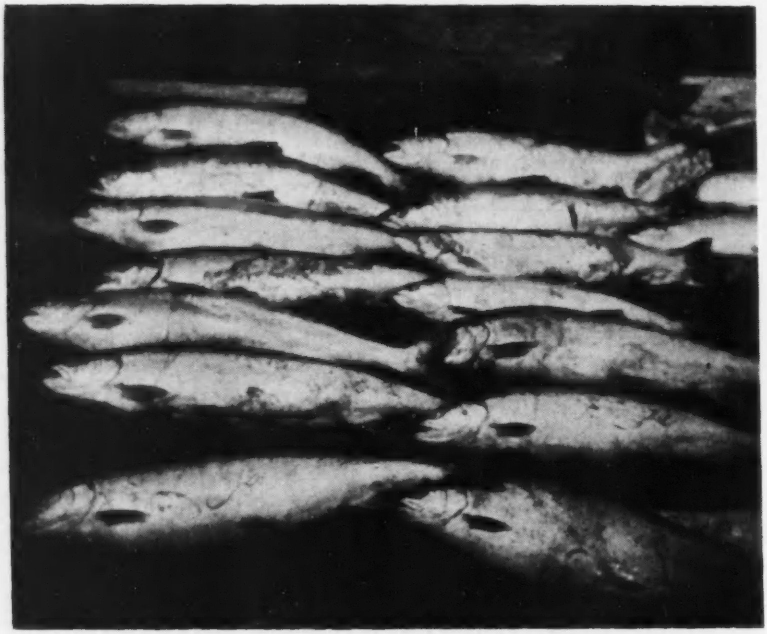

FIGURE 2.—Arctic char of commercial size taken by gill-nets at Nain.

six or seven men, and fishing exclusively for char from early July until mid-August, took the catches shown in Table II during four years.

The venture, located at one place, ceased in the fourth year because of the decline in production during the latter two years, with approximately the same fishing effort. This suggests that the Nachvak population was a local one and may have been fished too intensively in the first two years.

The above crew used 4½-inch stretched mesh gill-nets, each of which measured 180 to 210 feet (55 to 64 m.) in length and about 5 feet (1.5 m.) in depth. Nets set in coves during the sea-run always gave best fishing results. Here the nets were set at right angles to the shore line and generally in water about 6 feet (2 m.) deep. Twelve such nets fishing simultaneously took as many as 36 barrels, or approximately 3,000 fish, in one day.

According to local residents, as soon as the river ice breaks in the spring, Arctic char begin entering the sea. From this time and through the summer they are taken in gill-nets set in estuaries, coves, around headlands, and for some distance at sea. The *Patriot* crew reported that the peak fishing period was generally around the end of July at which time, presumably, the total run was in the sea. Fishermen say, too, that there is a lull in the fishing between the outward migration and the return migration to the river. The *Patriot* crew further reported

FIGURE 3.—Eskimo hauling Arctic char net near Nain.

taking the largest fish (10 to 14 lb.) near river mouths. Toward the end of the season char are reported to enter the river at high tide, with the larger fish in advance.

AGE DETERMINATIONS

Otoliths were used for age determination; these were removed from the dry fish head after return from the field. The otoliths were then cleaned, mounted in glycerine and water, and read in transmitted light using a standard binocular microscope. Right and left otoliths were read except in cases of doubt where one or both otoliths were discarded.

In the otolith, wide opaque bands alternate with narrow hyaline bands. The opaque bands are considered to represent summer growth and the hyaline bands the slower growth of winter. The centre of the otolith is considered to represent embryonic and early larval growth; this area appears hyaline except where cracks occur at the centre in which case the central area, either wholly or in part, appears opaque. The hyaline central area is followed by the first opaque band of summer growth and this in turn is followed by the first hyaline band of winter growth. The hyaline winter bands were counted and expressed in years: the growth of the last summer is expressed as plus growth for each reading, thus 7+ represents seven winters plus the summer growth of the year in which the sample was taken. Otoliths taken from fish of different ages and photographed in reflected light are shown in Figure 4.

Table III shows the age frequencies and the mean age of all samples. At Adlatok, the most southerly sample, the greatest number was in the 7-year age-class; at Nain, Okkak Bay, and Hebron, in the 9-year age-class; and at Ramah the

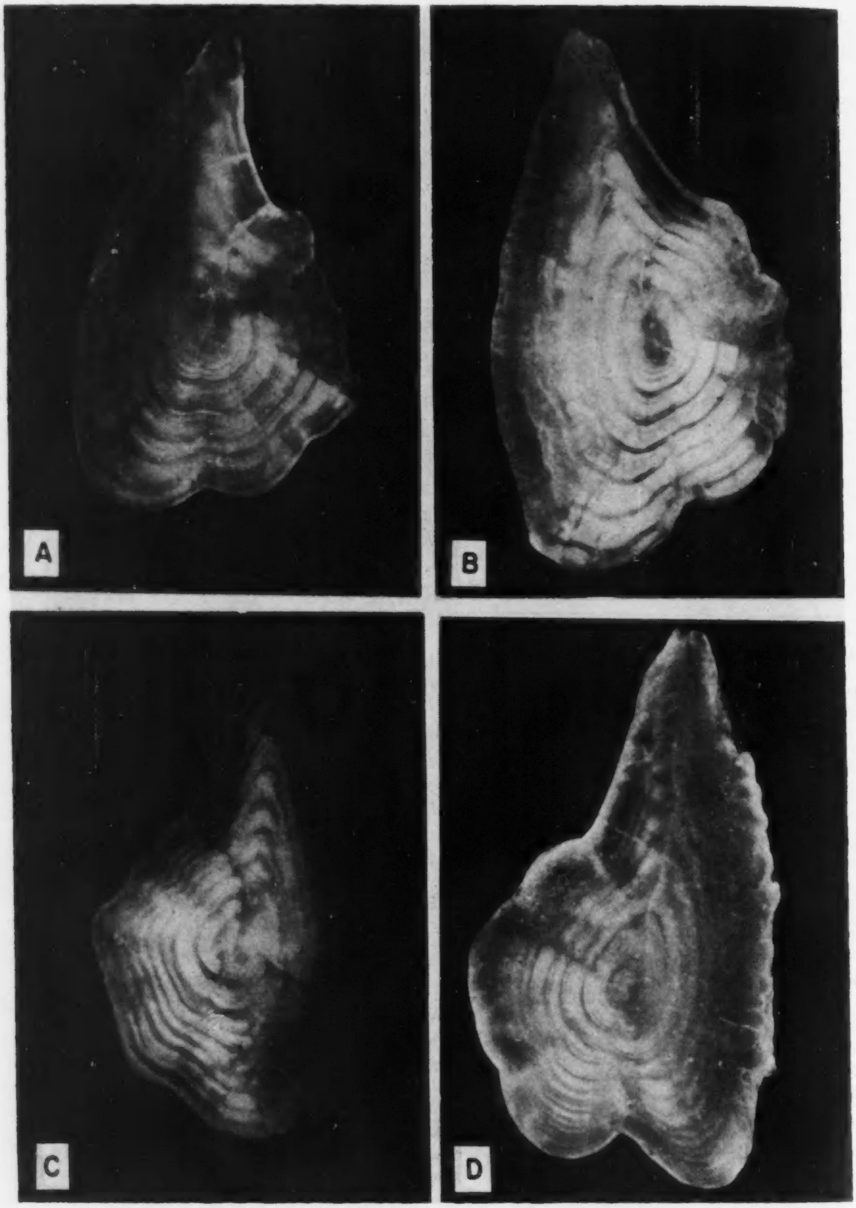

Figure 4.—Otoliths from Arctic char of different ages showing summer (light) and winter (dark) bands. (A) 6-year old; (B) 7-year old; (C) 9-year old; (D) 14-year old.

TABLE III.—Age composition of Arctic char in northern Labrador, July–August, 1953.

Locality	Age in years completed												Total fish	Mean age	Standard deviation	Standard error
	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+				
	numbers of fish													*years*	*years*	*years*
Adlatok	1	6	23	20	9	16	7	2	2	...	...	...	86	8.5	1.71	0.18
Nain	...	3	18	24	32	19	9	7	1	0	0	0	113	8.9	1.51	0.14
Okkak Bay	...	...	3	15	31	24	25	9	10	0	0	1	118	10.2	1.61	0.15
Hebron	...	...	1	6	19	16	8	6	11	3	...	...	70	10.5	1.77	0.21
Ramah	...	...	4	14	17	24	17	20	6	2	5	1	110	10.5	1.97	0.19

TABLE IV.—Weight composition of undressed Arctic char in northern Labrador, July–August, 1953. Percentages have been rounded. Standard deviations and standard errors have been calculated from the actual frequencies.

Locality	Proportion of total sample in various weight-classes									No. of fish	Mean weight	Standard deviation	Standard error
	1 lb.	2 lb.	3 lb.	4 lb.	5 lb.	6 lb.	7 lb.	8 lb.	9 lb.				
	%	%	%	%	%	%	%	%	%		*lb.*	*lb.*	*lb.*
Adlatok	...	16	20	22	14	16	3	8	1	90	4.4	1.810	0.191
Nain	16	43	26	13	1	1	...	...	...	121	2.5	1.041	0.095
Okkak Bay	25	47	21	6	1	...	...	...	...	120	2.1	0.874	0.080
Hebron	3	38	32	17	7	2	0	1	...	120	2.9	1.151	0.105
Ramah	10	55	21	8	2	2	1	0	1	120	2.5	1.223	0.112

greatest number was in the 10-year age-class. The mean age increases progressively with increase in latitude: at Adlatok (55°20′N.), it was 8.5, at Ramah (58°52′N.), it was 10.5 years.

The age distributions at Adlatok and Nain were significantly different from those of Okkak Bay, Hebron, and Ramah. There were no significant differences between the distributions at Adlatok and Nain nor between Okkak Bay, Hebron, and Ramah. The southern samples, Adlatok and Nain, average about 1½ years younger than the more northerly samples. Present information does not offer a complete explanation of these age differences either as differences in fishing effort or age at entering the sea. However, from a geographical as well as ecological point of view Adlatok and Nain may be regarded as distinct from Okkak Bay, Hebron and Ramah in the north. The former lie in sheltered waters, whereas the latter, except for Okkak Bay, are exposed to the open coastline and in direct contact with the cold Labrador Current. In the north the lakes and relatively short streams lie among the towering Torngat Mountains which, with their peaks approaching 6,000 feet, skirt the coastline from the Mugfords almost to Cape Chidley. In the Nain-Adlatok area elevation is much less, and the rivers, streams, and lakes penetrate far into the interior of Labrador.

WEIGHT DISTRIBUTION

Table IV shows that the 2- to 6-lb. weight-classes were well represented in the sample at Adlatok; the high frequency of 5-, 6-, and even 8-lb. fish in this area is, in all probability, due to the fact that other avenues of employment have been open to the fishermen of Hopedale in recent years and as a result fishing for Arctic char has been far less intensive than formerly.

The greatest numbers at all other places were in the 2- and 3-lb. classes and, in addition, Okkak Bay had the highest number of 1-lb. fish, namely 25%. The mean weight of the Adlatok sample was 4.4 lb. with a general decrease proceeding north to Okkak Bay where the mean weight was 2.1 lb. The Hebron and Ramah samples were exceeded only by Adlatok in mean weight.

The difference in weight between undressed and dressed fish varied from 0.3 lb. at the lower end to 0.8 lb. at the upper end of the weight range.

LENGTH FREQUENCIES

Fork-length measurements are shown in Table V where the fish are grouped at 5-cm. intervals; the total length range was 30.0–79.9 cm.
At Adlatok the modal class was 55.0–59.9 cm., while at Nain and places farther north it was always less; the smallest fish, however, were taken at Okkak Bay.

AGE–LENGTH RELATIONSHIP

Mean fork lengths for each age-group in all samples are shown in Figure 5 and Table VI. At ages 6–9 years mean length decreases with increase in latitude, but Hebron is an exception in this trend. At Adlatok for example, 8-year-old char

TABLE V.—Length composition of Arctic char in northern Labrador, July–August, 1953. Percentages have been rounded. Standard deviations and standard errors have been calculated from the actual frequencies.

Length group	Percentage fish in each length group				
	Adlatok	Nain	Okkak Bay	Hebron	Ramah
cm.	%	%	%	%	%
30.0–34.9	...	...	1	...	...
35.0–39.9	...	3	6	1	5
40.0–44.9	4	20	46	10	30
45.0–49.9	20	36	27	45	36
50.0–54.9	19	28	16	34	21
55.0–59.9	35	10	3	8	3
60.0–64.9	14	3	1	2	2
65.0–69.9	8	...	...	...	2
70.0–74.9	...	...	...	...	...
75.0–79.9	...	...	...	...	1
Total fish	92	121	120	120	120
Mean length, *cm.*	55.3	48.8	45.5	49.5	47.6
Standard deviation	6.545	5.380	5.045	4.377	6.410
Standard error	0.682	0.489	0.461	0.400	0.585

TABLE VI.—Age–length relationship of Arctic char, northern Labrador, 1953. (Figures in parentheses indicate the number of fish in each year-class.)

Age	Mean length				
	Adlatok	Nain	Okkak Bay	Hebron	Ramah
years	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*
5	44.5 (1)	...	...	...	...
6	48.2 (6)	39.8 (3)	...	...	...
7	49.9 (23)	44.9 (17)	41.8 (3)	47.0 (1)	41.2 (4)
8	55.7 (20)	47.6 (24)	44.0 (15)	47.6 (6)	42.3 (14)
9	57.0 (9)	49.7 (32)	45.4 (31)	48.7 (19)	44.2 (17)
10	58.4 (16)	50.1 (19)	45.3 (24)	49.5 (16)	47.2 (24)
11	62.6 (7)	50.6 (9)	45.0 (25)	50.6 (8)	47.8 (17)
12	62.5 (2)	54.2 (7)	47.4 (9)	51.4 (6)	49.5 (20)
13	65.6 (2)	54.2 (1)	48.2 (10)	51.5 (11)	50.3 (6)
14	...	...	...	47.6 (3)	60.8 (2)
15	...	...	...	...	57.1 (5)
16	...	...	62.0 (1)	...	76.4 (1)

had a mean length of 55.7 cm., while at Ramah, 212 nautical miles farther north, the same age-group was 13.4 cm. shorter.

At Hebron, at least for the year-classes sampled, growth conditions seem to be more favourable than at Ramah which is only 39 miles farther north, and much more favourable than at the place in Okkak Bay, 50 miles south of Hebron, where our sample was taken.

In the 10- to 13-year-old fish, decrease in length with increase in latitude is again seen, but among the older age-groups Okkak Bay has the slowest growth rate on the coast.

These observations indicate a general decrease in rate of growth from south to north but there are exceptions at Hebron and Okkak Bay.

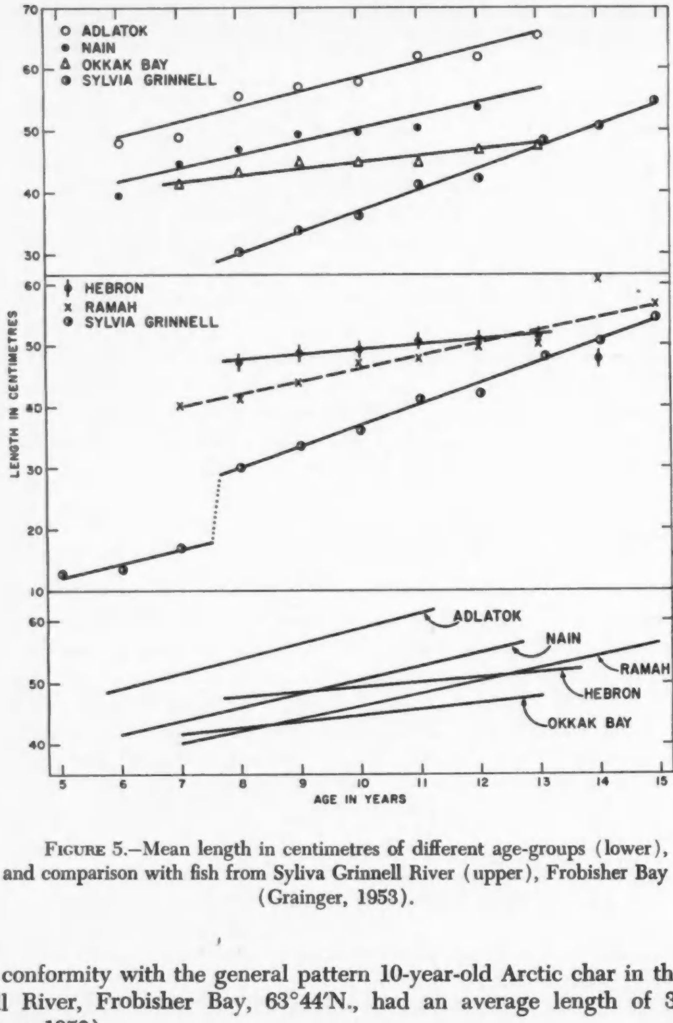

FIGURE 5.—Mean length in centimetres of different age-groups (lower), and comparison with fish from Syliva Grinnell River (upper), Frobisher Bay (Grainger, 1953).

In conformity with the general pattern 10-year-old Arctic char in the Sylvia Grinnell River, Frobisher Bay, 63°44′N., had an average length of 36.3 cm. (Grainger, 1953).

The Labrador char were caught with standard 4½-inch mesh used along the coast. Thus, among the younger age groups, 5 and 6 years, the mean length is biased upward since the larger fish in these age-groups are likely to be selected. On the other hand, among the older age-groups, to a lesser extent perhaps, the mean length is biased downward since the smaller fish in these age-groups are likely to be selected. The curve for Sylvia Grinnell River fish (from Grainger's data, 1953) is more representative of the fish in that area since a variety of mesh

sizes were used. The low growth rate of the Sylvia Grinnell char in the early ages (5, 6, and 7 years) is due, in all probability, to the fact that these fish, for the most part, had not gone to sea.

LENGTH–WEIGHT RELATIONSHIP

Figure 6 and Table VII show the relationship between length and undressed, as well as dressed, weights. All samples have been combined. The fish were grouped at 1-cm. intervals and the average weight of all fish within the centimetre interval is shown, thus each point on the graph is based on an average of from 3 to 44 fish.

When mean fish length is plotted against mean weight on double logarithmic paper a straight line relationship for undressed as well as dressed fish is obtained; from this relationship the following equation is obtained for undressed fish:

$$\text{Log } W = 3.125 \log L - 4.803$$

and for dressed fish:

$$\text{Log } W = 3.268 \log L - 5.121$$

TABLE VII.—Length–weight relations in Arctic char, northern Labrador, July–August, 1953. All samples are combined.

Length range	No. of fish	Average weight		Weight range		Calculated weight	
		Undressed	Dressed	Undressed	Dressed	Undressed	Dressed
cm.		*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*
37.0–37.9	5	1.3	1.0	1.2–1.5	1.0–1.2	1.3	1.1
38.0–38.9	3	1.5	1.2	1.2–1.7	1.0–1.5	1.4	1.2
39.0–39.9	11	1.6	1.2	1.0–2.0	0.7–1.5	1.5	1.2
40.0–40.9	20	1.7	1.3	1.0–2.0	0.8–1.7	1.7	1.3
41.0–41.9	16	1.8	1.5	1.5–2.2	1.2–1.7	1.8	1.4
42.0–42.9	27	1.9	1.5	1.5–2.2	1.2–1.9	1.9	1.6
43.0–43.9	34	2.1	1.7	1.5–2.4	1.5–2.0	2.1	1.7
44.0–44.9	38	2.2	1.8	1.7–4.1	1.2–3.7	2.2	1.8
45.0–45.9	33	2.4	2.0	2.0–3.0	1.5–2.6	2.4	2.0
46.0–46.9	43	2.5	2.1	2.0–3.0	1.7–2.5	2.5	2.1
47.0–47.9	41	2.8	2.3	2.2–3.2	1.9–2.7	2.7	2.3
48.0–48.9	39	2.9	2.4	2.0–3.7	1.8–3.0	2.9	2.4
49.0–49.9	44	3.0	2.5	2.5–3.7	2.0–3.2	3.1	2.6
50.0–50.9	39	3.1	2.8	2.5–3.8	2.5–3.3	3.3	2.8
51.0–51.9	36	3.6	2.9	3.0–4.6	2.0–3.5	3.5	2.9
52.0–52.9	28	3.9	3.3	3.0–4.8	2.5–4.0	3.7	3.2
53.0–53.9	22	4.0	3.3	2.7–4.5	2.5–4.2	4.0	3.4
54.0–54.9	21	4.2	3.6	2.5–5.0	2.2–4.2	4.2	3.6
55.0–55.9	22	4.4	3.9	3.0–5.2	2.7–4.7	4.4	3.8
56.0–56.9	12	4.7	4.1	3.7–5.7	3.0–4.7	4.7	4.0
57.0–57.9	11	5.0	4.5	4.6–5.8	3.5–5.0	5.0	4.0
58.0–58.9	9	5.7	5.0	4.7–6.6	4.0–6.0	5.2	4.5
59.0–59.9	7	5.5	5.1	4.7–6.3	4.0–6.0	5.5	4.8
60.0–60.9	7	6.2	5.6	5.5–6.7	4.5–6.1	5.8	5.0
61.0–61.9	1	7.5	6.6	...	...	6.1	5.3
62.0–62.9	6	6.1	5.4	4.2–6.9	3.7–6.5	6.4	5.6
63.0–63.9	4	7.6	6.7	7.0–8.0	6.0–7.0	6.7	5.9
64.0–64.9	4	7.7	7.0	6.2–9.0	5.7–8.0	7.1	6.2
65.0–65.9	4	6.8	6.1	5.2–8.2	4.5–7.8	7.5	6.5
66.0–66.9	5	7.8	7.0	6.0–8.9	5.0–8.2	7.8	6.9

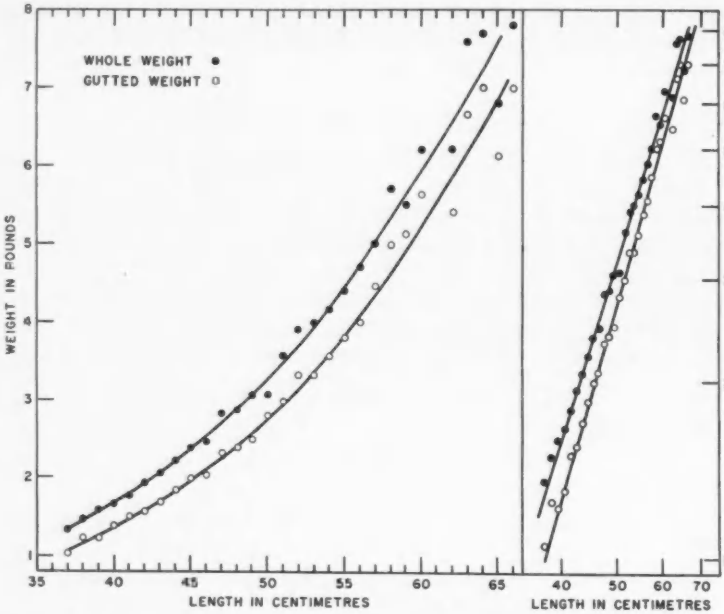

FIGURE 6.—Length–weight relations in undressed and dressed char, all samples combined. Arithmetic plot on the left, logarithmic plot on the right.

VERTEBRAL COUNTS

The vertebral counts are from the atlas to the last caudal centrum, inclusive. A lateral view of the caudal skeleton showing the last two centra is shown in Figure 7.

Counts were made in the laboratory on cleaned vertebral columns. The first count was checked by a second investigator and random counts in each sample were made as a third and final check.

The vertebrae ranged in number from 63 to 69 (Table VIII). Although fluctuations occurred the mean numbers show a general increase with increase in latitude from 65.45 at Adlatok to 66.47 at Hebron. The differences between the

TABLE VIII.—Vertebral frequencies of Arctic char taken in northern Labrador, July–August, 1953.

Locality	Number of vertebrae 63	64	65	66	67	68	69	Total No. of fish	Mean vertebral No.	Standard deviation	Standard error
Adlatok	4	7	38	29	12	1	...	91	65.45	1.003	0.105
Nain	...	8	37	49	23	3	1	121	65.82	0.955	0.087
Okkak Bay	2	10	36	40	24	4	...	116	65.74	1.048	0.097
Hebron	...	...	15	50	36	14	2	117	66.47	0.925	0.080
Ramah	...	1	25	45	32	9	3	115	66.28	1.027	0.094

more distant localities are statistically significant, but the differences beween the vertebral averages of the Nain–Okkak Bay or the Hebron–Ramah samples are not significant.

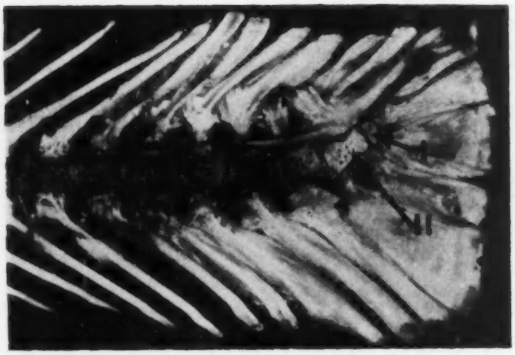

FIGURE 7.–The caudal skeleton showing last two vertebrae counted–I and II.

FIN RAY COUNTS

For purposes of counting, fin rays *in situ* were stripped of skin at the base and read against a light placed underneath. All fin rays visible to the naked eye were counted. At the anterior end of the dorsal fin are found 3 or 4 short unbranched rays; the first, and sometimes the second are not always easily recognized. The last two branched rays are based on the same radial bone and were counted as one fin ray. The anal fin begins with one or two short rays, and as in the case of the dorsal, the last two branched rays, which arise from the same base, were counted as one. In the pelvic fin there is a single short ray at the anterior end.

Table IX shows the fin ray count for dorsal, pectoral, pelvic, and anal fins. In general, there was an increase in the mean count for each fin with increase in latitude.

The mean numbers of fin rays indicate a significant difference between the Adlatok and Ramah samples; these are from the extremes of our range of sampling. Within the range significant differences are indicated between Adlatok and Okkak Bay by the pelvic and anal fins only, and between Okkak Bay and Ramah samples by the dorsal and pectoral fins only. Also, only the pectoral and pelvic fins indicate a difference between the Nain and Hebron fish. No significant difference is indicated by any fin for the Nain and Okkak Bay fish, and only the pectoral shows a difference between Okkak Bay and Hebron and between Hebron and Ramah fish.

Vladykov (1954) observed an average fin ray count of 11.0 for the dorsal fin of 17 specimens of *Salvelinus alpinus* from widely separated localities; this is considerably less than our minimum mean count of 14.34 for 103 fish at Okkak Bay.

TABLE IX.—Fin ray count in dorsal, pectoral, pelvic and anal fins from Arctic char taken in northern Labrador, July–August, 1953. (Number of rays in bold.)

Fin and locality	Fin-ray frequencies					Total number of fish	Mean fin-ray number	Standard deviation	Standard error
Dorsal:	**12**	**13**	**14**	**15**	**16**				
Adlatok	...	8	46	41	5	90	14.44	0.720	0.075
Nain	...	11	48	35	6	83	14.36	0.758	0.083
Okkak Bay	...	12	45	40	3	103	14.34	0.721	0.071
Hebron	...	7	39	45	9	91	14.56	0.748	0.077
Ramah	...	4	29	55	12	117	14.74	0.721	0.061
Pectoral:	**12**	**13**	**14**	**15**	**16**				
Adlatok	1	39	57	3	...	74	13.61	0.569	0.066
Nain	2	21	68	9	...	116	13.85	0.593	0.055
Okkak Bay	2	26	56	16	1	120	13.77	0.725	0.072
Hebron	...	10	62	28	...	93	14.18	0.589	0.061
Ramah	...	20	65	15	...	117	13.96	0.593	0.051
Pelvic:	**9**	**10**	**11**	**12**	**13**				
Adlatok	5	87	8	...	...	74	10.03	0.372	0.043
Nain	7	84	13	...	...	113	10.11	0.385	0.036
Okkak Bay	1	83	16	...	...	119	10.15	0.386	0.038
Hebron	2	65	25	1	...	93	10.27	0.513	0.053
Ramah	...	84	16	...	...	117	10.16	0.370	0.034
Anal:	**11**	**12**	**13**	**14**	**15**				
Adlatok	2	16	66	16	...	62	12.97	0.626	0.078
Nain	...	18	57	22	3	116	13.10	0.672	0.062
Okkak Bay	...	8	61	29	2	111	13.24	0.621	0.058
Hebron	1	15	48	35	1	86	13.19	0.744	0.082
Ramah	...	10	53	36	1	116	13.28	0.654	0.060

FLESH COLOUR

A characteristic feature of the Arctic char of northern Labrador, at least during June, July, and August, is that the fish vary in flesh colour, being classified as white, pink, and red; the colours intergrade somewhat, consequently variation in grading is possible especially between pink and red. For purposes of marketing, red is in highest demand, pink is in lesser demand and receives a lower price, while white-fleshed char have not been marketed since 1949; instead, the latter are hung on poles and dried in the open air during summer weather to be used as food for the local residents.,

The percentage of white-, pink- and red-fleshed char for our samples is shown in Table X. No white muscle is reported for Hebron and Ramah, nor for the small Nain (2) sample. White-fleshed char were most common in Okkak Bay.

TABLE X.—Percentage of white-, pink-, and red-fleshed char from northern Labrador, 1953.

Locality	Date	White	Pink	Red	No. of fish
		%	%	%	
Adlatok	Aug. 10	9	84	7	89
Nain (1)	July 17	7	43	50	117
Nain (2)	Aug. 7	0	39	61	31
Okkak Bay	July 23	23	49	29	120
Hebron	July 30	0	56	44	120
Ramah	Aug. 3	0	64	36	120

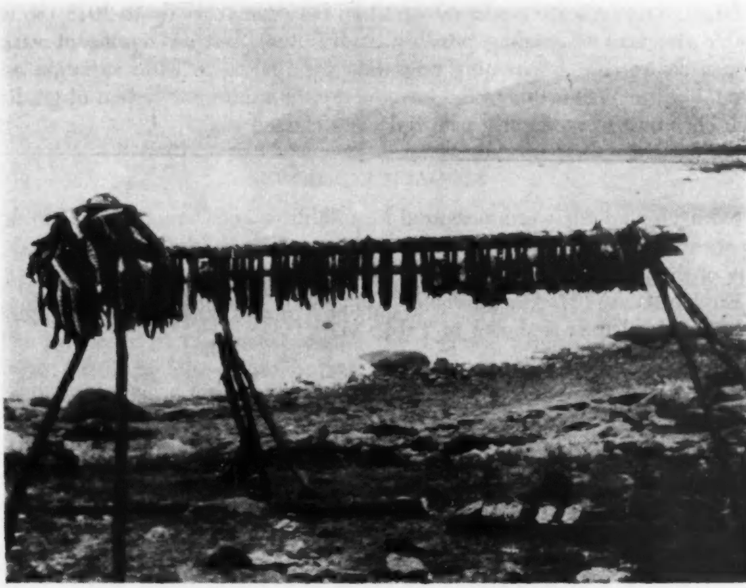

FIGURE 8.—Drying white-fleshed char at Okkak Bay.

The percentage of pink flesh was highest at Adlatok, Hebron and Ramah were next in order, while Okkak Bay and Nain were lowest.

It is generally believed along the northern Labrador coastline that red-fleshed char predominate at Hebron and places farther north, such as Nachvak. Our samples, however, show the highest percentage of red fish at Nain, followed by Hebron and Ramah, and fewest at Adlatok.

No statistics are available to show flesh colour percentages throughout the season at any one place. The Adlatok sample (Table X) was netted in an estuary quite near the river mouth and therefore represents fish about to enter the river. Data provided by the Newfoundland Department of Public Welfare agent at Okkak Bay (Table XI) show the percentage of white, pink, and red during 1944–49 for the seaward migration and for the spawning migration of 1948 at Okkak Bay.

TABLE XI.—Percentage of white-, pink-, and red-fleshed char at Okkak Bay, 1944–49.

Colour	Seaward migration						Spawning migration
	1944	1945	1946	1947	1948	1949	1948
	%	%	%	%	%	%	%
White	8	23	31	15	18	27	16
Pink	27	28	25	26	29	55	30
Red	65	49	44	59	53	18	54
Total landings, *cwt.*	129	182	227	441	471	190	559

These data indicate moderate variation between years up to 1948 (to which variable standard of grading possibly contributes), but no significant variation between seaward and spawning migration for 1948. The wide variation among pink and red in 1949 is due to the introduction of a different system of grading in which char that were slightly pale red were classed pink.

STOMACH CONTENTS

Stomach contents were measured in millilitres; chief among the food organisms were: capelin (*Mallotus villosus*), launce (*Ammodytes americanus*), the young of the mailed sculpin (*Triglops pingeli*), Amphipoda (*Themisto libellula*) and Euphausiacea (*Meganyctiphanes norvegica*). The percentage by volume of the various foodstuffs is shown in Table XII.

TABLE XII.—Percentage of various food organisms found in stomach contents from Arctic char in northern Labrador, July–August, 1953.

Station	No. of fish	Empty stomachs	Total volume of food	Percentage by volume				
				Capelin	Launce	Amphipoda & Euphausiacea	Sculpins	Unidentified
		%	ml.	%	%	%	%	%
Adlatok	94	92.6	67	88.0	3.0	0	0	9.0
Nain (1)	119	9.2	3,095	75.2	10.7	13.5	0	0.6
Nain (2)	31	16.1	433	15.0	12.7	11.1	61.2	0.2
Okkak Bay	120	15.0	2,829	99.3	0.2	0.5	0	0
Hebron	119	4.2	5,522	2.9	0.3	81.3	14.9	0.6
Ramah	120	2.5	5,098	3.9	13.5	56.2	24.7	1.7

Capelin formed the chief source of food at Adlatok. However, most of the fish had empty stomachs. Capelin were also the chief food in the Nain (1) and Okkak Bay samples. In the shallower coastal waters such as at Nain, Adlatok and Okkak Bay, capelin come inshore to spawn. At Hebron and Ramah, however, the absence of spawning grounds may explain the lack of capelin in the diet. In the Nain (2) sample, capelin had, in all probability, returned to the deeper offshore waters after spawning.

In the Nain (2) sample, taken three weeks later than the Nain (1) sample, young mailed sculpins formed the bulk of the food. Sculpins were also present in the Hebron and Ramah samples. Amphipoda and Euphausiacea were the most important food items at Hebron and Ramah.

PARASITES

The Arctic char were found to be parasitized with roundworms (*Philonema* sp.) and tapeworms (*Eubothrium salvinale*). The percentage infestation at the various stations is shown in Table XIII.

Adult *Philonema* were taken from the body cavity only, but immature stages of roundworms, for which the species was not determined, were encysted in the liver, gonads, spleen, peritoneum, and viscera in general. None was observed

TABLE XIII.—Degree of infestation (per cent) in Arctic char in northern Labrador, 1953.

Station	*Philonema sp.*	*Eubothrium salvinale*	Number of fish
	%	%	
Adlatok	4	87	90
Nain (1)	41	95	121
Nain (2)	61	97	31
Okkak Bay	31	90	120
Hebron	42	45	120
Ramah	52	96	120

in the muscle. The tapeworms were confined to the intestinal tract, chiefly in the duodenum and pyloric caeca, but also in the lower intestine.

The incidence of *Philonema* among the different samples was indicated by an arbitrary scale as follows: none; light, 1 to 5 worms; medium, 6 to 12 worms; and heavy, 13 or more. The extent of infestation by *Eubothrium* was determined on the basis of volume occupied by the proglottids. The degree of infestation by each is shown in Table XIV.

In general, *Philonema* infestation was light, except at Nain. *Eubothrium* infestation was heavy in all samples except at Hebron.

TABLE XIV.—Char classified as to intensity of parasitization by *Philonema* and *Eubothrium*. Figures shown are the percentages of each of the classes as defined in the text.

Station	*Philonema*				*Eubothrium*			
	None	Light	Medium	Heavy	None	Light	Medium	Heavy
	%	%	%	%	%	%	%	%
Adlatok	97	3	...	...	13	30	26	31
Nain (1)	41	30	12	17	3	29	36	32
Nain (2)	39	23	26	13	3	7	16	74
Okkak Bay	67	28	3	2	9	28	27	36
Hebron	55	37	7	1	54	35	8	3
Ramah	48	33	16	3	5	7	14	74

SUMMARY

1. Arctic char (*Salvelinus alpinus* L.) in northern Labrador were sampled from the commercial sea-run catch at Adlatok, Nain, Okkak Bay, Hebron, and Ramah.

2. In northern Labrador Arctic char form an important source of food and income for the native population.

3. In the Adlatok–Nain area Arctic char enter the commercial fishery at 5 to 6 years of age; at Okkak Bay, Hebron, and Ramah, commercial size is reached about 1 year later and there is a tendency for the average age to increase as one proceeds north to Ramah. The dominant age group for Adlatok is 7 years; for Nain, Okkak Bay, and Hebron, 9 years; and Ramah, 10 years.

4. The mean undressed weight of Adlatok fish was 4.4 lb., and Okkak Bay 2.1 lb.; other stations had intermediate undressed weights. The mean fork length ranged from 55.3 cm. at Adlatok to 47.5 cm. at Okkak Bay.

5. In a given age-group covering all samples the mean length, in general, decreased with increase in latitude, but there were variations in this tendency, particularly at Okkak Bay where the older fish had the slowest growth.

6. The mean vertebral and fin ray counts tended to increase with increase in latitude; a significant difference between the means is indicated for the Adlatok–Ramah, Nain–Hebron, and Okkak Bay–Hebron samples.

7. White-, pink-, and red-coloured flesh are characteristic of the char of Labrador. The incidence of white-coloured flesh was relatively high in the Okkak Bay sample and low in all others. Pink-coloured flesh constituted at least one half the samples except at Nain; red-coloured flesh was high at Nain, low at Adlatok with intermediate incidence at Hebron, Ramah, and Okkak Bay.

8. Capelin, launce, young mailed sculpins, Amphipoda and Euphausiacea formed the bulk of the stomach contents.

9. Parasites of the genus *Philonema* sp. and *Eubothrium salvinale* were observed in all areas in varying degrees of intensity.

ACKNOWLEDGMENTS

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Spoilage of Fish in the Vessels at Sea: 5. Bilgy Fish[1,2]

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ABSTRACT

Offensive "bilgy" odours develop when fish are stored in contact with slime-soaked wooden surfaces. Anaerobic bacteria develop in the slime layer between the surfaces of the fish and the wood.

The muscle of bilgy fish has a higher hydrogen sulphide and a lower mercaptan content than that of similar fish spoiling in ice but not in contact with wood. The trimethylamine and volatile acid values are usually, but not consistently, high in bilgy fish.

In the observations described in this paper, the fillets of fish stored in contact with dirty pen boards acquired a distinct bilgy odour when the anaerobic bacteria on the skin exceeded 10^6 per cm.^{2}, at which point the hydrogen sulphide content of the muscle was 0.05 mg. or more per 100 g. of fish.

INTRODUCTION

During the last 3 or 4 years a type of spoilage commonly referred to as "bilgy fish" has been increasingly brought to our attention. There is reason to believe that although this type of spoilage has always been present to some degree, it has for a reason pointed out below become of special significance following the widespread production of frozen fish "blocks" for the manufacture of fish sticks.

The term "bilgy fish" was adopted by the fishermen because of their belief that the trouble developed only when the fish came in contact with the drainage of bilge water that collects in the bottom of the vessel. The fishermen were quite right in observing the very close resemblance between the odour of bilgy fish and the odour that develops as bilge water decomposes; they were wrong, however, in assuming that one was the cause of the other.

It has been shown previously by Castell (1954) and MacCallum (1955) that this type of spoilage arises most often when fish are left in direct contact with slime-soaked wooden boards. This occurs at sea when fish are stored in direct contact with the wooden pen boards, but may also occur after the fish have been discharged and are held in storage in wooden pens or boxes in the plant.

It can be easily demonstrated that contact with bilge water is not the cause of bilgy fish. First, it can be observed that, high up in the pens, in locations where it would be quite impossible for bilge water to come in contact with them, fish stored against the boards do become bilgy. More direct evidence was obtained by experiment: A batch of similar fish was divided into two lots. Bilge water was poured over one lot and the remainder was securely fastened between pen boards.

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Both lots were then stored in chipped ice. Within 24 hours the fish treated with bilge water had lost their offensive odour and subsequently spoiled without becoming bilgy. The fish stored in ice between the pen boards gradually developed the characteristic odour of the putrid bilge water or typical bilgy fish.

Observations made during the last 3 years have suggested several important characteristics of bilgy fish. The substance responsible for the offensive odour is either very volatile or very rapidly oxidized by exposure to the atmosphere. During the earlier stages of its development, before the odours have become very intense, a short exposure to the air frequently eliminates the odour altogether. Slightly bilgy cod and haddock fillets shipped from Halifax to central Canada have reached the retail markets entirely free from bilgy odours.

Freezing, on the other hand, locks in the offensive odours. This is of particular significance in the use of frozen blocks of fillets for fish stick production, where in the sawing of the frozen blocks the bilgy odour is temporarily intensified by the frictional heat developed. Frozen bilgy fillets examined after 12 months' storage were still offensive when defrosted. Frequently, however, fish that were only mildly bilgy at defrosting became odourless after standing for a short while at room temperature.

It has never been observed that fillets cut from bilgy fish have become progressively more bilgy on standing.

When a bilgy fillet is immersed in an acid solution, the odour becomes intensified and sometimes slightly changed; in an alkaline dip the odour is either eliminated or greatly reduced.

Preliminary tests made on typical bilgy fish taken from trawlers have shown that the rise in the trimethylamine value that usually accompanies the earlier stages of spoilage of cod and haddock does not always occur. Highly offensive bilgy haddock, for instance, have been observed with trimethylamine values of less than 2 mg. of trimethylamine nitrogen per 100 g. of muscle. Similarly it has been observed that the pH of bilgy fish may occasionally be comparable to that of first grade fresh fish (i.e. pH 6.2 to 6.5 for haddock).

The work described in this paper is a continuation of these earlier attempts to define bilgy fish, with the object of finding if possible some objective criterion by which bilginess may be chemically identified and the degree of spoilage measured. The bacterial and chemical mechanisms involved in the production of the bilgy odours are discussed, but await further critical examination.

EXPERIMENTAL

Materials

Bilgy fish in various stages of development were obtained by placing freshly caught dressed cod or haddock between pen boards taken from a trawler. These were held secure with clamps or heavy iron wire. They were then buried in chipped ice. Similar fish, not in contact with the boards, were also buried in the ice for purposes of comparison. Periodically one or more fish of each group were taken out for examination and analysis.

The muscle samples used for chemical determinations were obtained by removing two fillets from each fish and chopping them into small sections with a sharp knife. These were well mixed and the required portions weighed out for each of the determinations: 100 g. each for trimethylamine, hydrogen sulphide, and mercaptans, and 10 g. for volatile acids. It had been found in preliminary tests that the usual method of macerating the fish muscle in a Waring blendor was not satisfactory for determinations of mercaptan or hydrogen sulphide.

Methods

Trimethylamine (TMA) values (used in this paper to indicate milligrams of TMA nitrogen per 100 g. muscle) were determined by Beatty and Gibbons' (1937) modification of Conway and Byrne's (1933) micro-diffusion technique.

The method described by Brenner, Owades and Golyzniak (1953) was used for determining hydrogen sulphide. This is a modification of the procedure suggested by Fischer (1883). The hydrogen sulphide was removed by a current of carbon dioxide acting on an aqueous, acidified solution of the fish extract. It was then absorbed in dilute zinc acetate and combined with *p*-amino dimethylaniline, hydrochloric acid and ferric chloride to form methylene blue, which was determined with an Evelyn colorimeter using a 660-mμ filter. This was essentially the procedure used by Almy (1925) for measuring hydrogen sulphide in fresh and spoiling meats and fish. The method of Fellers, Shostrom and Clarke (1924), which consisted of aerating an acidified solution and collecting the hydrogen sulphide in standard iodine, was also tried but found too insensitive for this type of analysis. Mercaptans were determined by the method of Brenner, Owades, Gutcho and Golyzniak (1954) and modified by Brenner, Owades and Fazio (1955).

Volatile acids were determined by Friedmann's method (1938).

Bacterial counts were restricted to the skin only. A piece of skin 4 by 4 cm. was cut from the side of the fish on the lateral line immediately beneath the middle of the dorsal fin. For counts of aerobic bacteria the medium described by Dyer, Dyer and Snow (1946) was used; for anaerobic bacteria Reed's modification of Brewer's medium (Reed and Orr, 1943) was employed using Brewer's anaerobic-type petri dishes. In this paper the term "anaerobic count" has been used to indicate the number of colonies developing on this particular medium and in these plates that are especially adapted for culturing anaerobic bacteria. No effort was made to distinguish absolute anaerobes and the facultative types. All plates were incubated at 25°C.

Results

Hydrogen sulphide, trimethylamine, and volatile acids

Table I gives the results of analyses of 30 fish that had been completely buried in ice for 1 to 18 days. These fish were not in contact with wooden surfaces

TABLE I.—Trimethylamine (TMA) values and other data on dressed cod and haddock that had been buried in ice from 1 to 18 days. The data have been arranged in order of descending TMA values.

Species[a]	TMA	Volatile acids[b]	pH	Fillet odour	Hydrogen sulphide	Days in ice
	mg./100 g.				*mg./100 g.*	
C	34	161	7.3	Putrid	0.075	18
H	33	118	7.1	Putrid	0.006	12
H	27	87	7.0	Putrid	0.002	9
C	21	22	7.1	Putrid	0.004	16
C	18	107	7.1	Putrid	0.004	14
H	16	...	6.6	Stale-musty	0.003	16
H	15	58	6.6	Sour-putrid	0.006	15
C	15	...	7.1	Fruity	0.008	11
C	12	49	6.8	Sour	0.002	7
H	12	12	6.6	Sour	0.003	7
C	10	60	7.0	Sour-putrid	0.016	10
H	10	30	6.6	Sour	0.004	7
C	6	34	6.8	Sour	0.002	7
H	6	13	6.6	Sour	0.005	6
H	5	...	6.6	Seaweedy	0.002	7
C	5	22	7.2	Slightly sour	0.009	13
C	4	18	6.9	Old cabbage	0.021	10
H	3	8	6.6	Slightly sour	0.021	2
H	3	7	6.5	Slightly sour	0.003	1
H	2.3	...	6.6	Seaweedy	0.003	2
H	1.8	...	6.5	Seaweedy	0.003	6
H	1.5	...	6.5	Seaweedy	0.003	3
C	1.5	10	6.9	Slightly sour	0.006	6
H	1.5	22	6.5	Neutral	0.003	5
C	1.5	11	6.8	Neutral	0.010	3
C	1.5	11	6.7	Neutral	0.006	1
C	1.5	8	6.8	Neutral	0.008	5
H	1.5	8	6.3	Neutral	0.010	2
H	1.0	17	6.5	No odour	0.006	3
C	0.7	9	6.7	No odour	0.020	3

[a]C indicates cod; H indicates haddock.
[b]Volatile acid is expressed as ml. 0.01 N NaOH per 100 g. fish muscle.

at any time during storage. The results have been arranged according to the TMA values in descending order.

It may be seen that this same order roughly held for the volatile acid values as well as for the degree of spoilage indicated by the fillet odours. It may also be seen that the hydrogen sulphide content of the muscle did not significantly increase as spoilage progressed.

Table II gives similar results for corresponding fish that were secured between pen boards before being buried in ice. These have been arranged according to descending order of their hydrogen sulphide values. This order corresponded approximately with their degree of spoilage as indicated by the odour from the fillets. The bilgy odours became evident only when the hydrogen sulphide content reached 0.04 to 0.1 mg. per 100 g. and strong when the values were above 0.1 mg. per 100 g. Table II also shows that there was a very poor correlation between the TMA values and the development of bilgy odours in the fish, the values ranging

TABLE II.—Hydrogen sulphide values and other data on dressed cod, pollock, and haddock that had been held between pen boards and stored from 1 to 14 days in ice. The data have been arranged in order of descending hydrogen sulphide values.

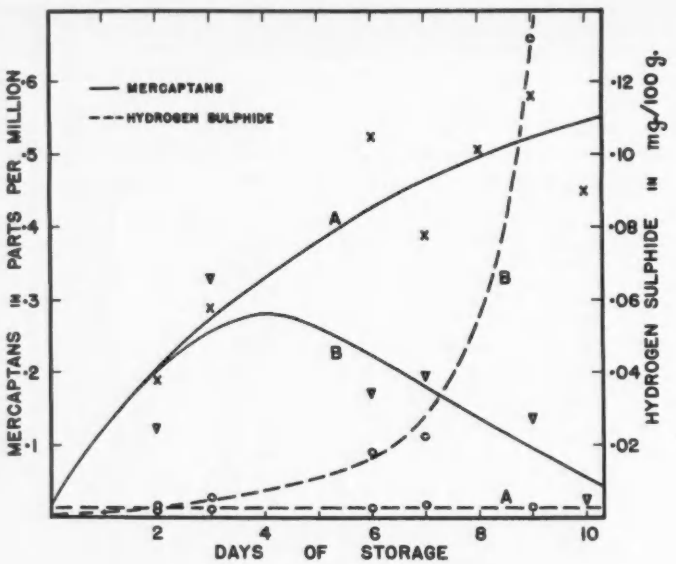
Species[a]	TMA	Volatile acids[b]	pH	Fillet odour	Hydrogen sulphide	Days in ice
	mg./100 g.				*mg./100 g.*	
H	33	213	6.7	Very bilgy	1.17	8
H	30	183	6.8	Very bilgy	0.73	9
H	7	34	6.7	Bilgy	0.58	6
C	96	118	6.9	Bilgy	0.52	7
H	6	39	6.7	Bilgy	0.50	7
C	8	94	6.9	Bilgy	0.40	13
C	102	86	6.9	Bilgy	0.26	7
C	...	300	...	Bilgy	0.18	7
C	9	30	6.9	Bilgy	0.17	10
H	35	...	7.0	Bilgy	0.13	9
C	36	475	6.9	Bilgy	0.13	7
H	1.5	15	6.5	Sl. bilgy	0.11	2
P	42	185	6.9	Sl. bilgy	0.08	14
C	4	20	7.0	Sl. bilgy	0.08	6
P	39	234	6.8	Fruity?	0.06	14
C	16	...	7.1	Bilgy	0.05	10
H	32	...	6.9	Bilgy	0.04	10
P	2	10	6.8	Very sl. bilgy?	0.03	4
H	25	...	6.8	Very sl. bilgy?	0.02	7
H	3	10	6.6	Sour-musty	0.02	2
H	24	...	6.8	Sour-cabbage	0.02	6
H	13	48	6.7	Sour	0.013	5
H	0.7	10	6.5	None	0.012	1
C	0.7	7	6.9	None	0.008	2
H	5	15	6.6	Sour	0.007	3
C	5	18	6.4	Sour	0.007	6
H	3	...	6.5	Seaweedy	0.006	3
C	1.5	15	6.8	Stale	0.005	5
H	3	...	6.6	Stale	0.003	1
H	1.9	...	6.1	Seaweedy	0.002	2

[a]C indicates cod; H indicates haddock; P indicates pollock.
[b]Volatile acid is expressed as ml. 0.01 N NaOH per 100 g. fish muscle.

from 1.5 to 102. Although there were exceptions, the bilgy fish as a group had higher volatile acid values than the fish that spoiled without contact with the pen boards.

MERCAPTANS

The accompanying Figure shows the curves for the production of mercaptans and hydrogen sulphide for fish stored in ice between boards and for similar fish not in contact with boards. The mercaptan curves for the two lots of fish are quite different. For the fish not in contact with the boards, the values continued to rise as storage was prolonged. For fish between boards, there was an initial rise followed by a gradual decrease. After 10 days the mercaptan content of the "normally" spoiling fish was approximately 18 times that of the corresponding bilgy fish. In other similar tests the results were the same, showing low mercaptan values for bilgy fish and high values for "normal" spoilage.



The mercaptan and hydrogen sulphide content of fillets cut from two lots of dressed haddock, one (A) that had been buried in ice, and one (B) that had been held in contact with pen boards in ice for periods up to 10 days.

AEROBIC AND ANAEROBIC BACTERIA

Pressing the slimy surface of the fish firmly against a wooden surface excludes the air and enables the bacteria present to bring about an anaerobic environment. From Table III it may be seen that anaerobic bacteria became much more numerous on the surface of the fish that have been jammed between the pen boards than on the surface of similar fish surrounded by ice.

Actually the difference was greater than the figures indicate, because in the case of the fish between the pen boards, large numbers of bacteria had adhered to the wooden surfaces, and hence were not determined in the test.

It is interesting to observe that once the anaerobic count reached 1,000,000 bacteria per square centimetre of skin, the muscle beneath acquired the characteristic bilgy odour. None of the fish between boards with anaerobic counts under a million were bilgy, even though the aerobic count in some cases was almost 100,000,000 per cm^2.

The earlier differences in the number of aerobic bacteria on the two groups of fish can probably be accounted for by the bacteria picked up by this fish from the heavily contaminated wood. Counts up to 50,000,000 per cm^2. have been obtained from the surface of "washed" pen boards and much higher counts from boards still retaining the surface slime.

TABLE III.—Numbers of aerobic and anaerobic bacteria from 38 fish stored from 1 to 14 days in ice. Nineteen of these fish were held firmly between pen boards while the remainder were completely surrounded by ice.

Days in storage	Anaerobic bacteria (thousands per square centimetre of skin)		Aerobic bacteria (thousands per square centimetre of skin)	
	Between boards	Surrounded by ice	Between boards	Surrounded by ice
7	52,000[a]	640	17,500	26,300
7	18,000[a]	200	5,000	2,500
14	10,400[a]	850	1,160,000	48,000
8	8,100[a]	625	15,300	246,000
13	8,000[a]	120	54,000	73,000
9	4,200[a]	4,700	109,000	66,200
13	3,200[a]	750	70,000	100,000
6	3,100[a]	14	2,000	1,400
7	2,200[a]	27	22,700	3,800
3	150	5	18,900	240
10	120	20	93,000	170
5	54	39	33,100	25,200
1	47	5	3,400	1,400
2	35	11	760	200
6	34	2	137	110
2	27	1	820	110
1	21	4	2,600	100
2	8	0.7	266	3
8	1.6	1.8	13,200	100

[a]The fillets cut from these fish had a bilgy odour.

DISCUSSION

It has long been known that in the absence of oxygen, many bacteria are able to reduce sulphates and other sulphur-containing compounds to hydrogen sulphide; and conversely that aeration induces bacteria to oxidize sulphydryl sulphur directly to sulphate. These are simply oxidation and reduction phases of the sulphur cycle brought about by micro-organisms. Such reactions are commonly encountered in the bacteriology of soil and sewage and in the decomposition of plant and animal tissue under different environmental conditions. It is not surprising therefore that similar reactions occur in the decomposition of fish muscle.

In general the results given in this paper support previous observations that during the earlier stages of spoilage of cod, haddock, herring and certain other sea fish, TMA and volatile acids accumulate rapidly and that during this phase little or no hydrogen sulphide is formed (Almy, 1925; Sigurdsson, 1947; Holmov, 1937; Tanikawa, 1938; Allison, 1948; Reay and Shewan, 1949; etc.). There are limitations to this general statement, however, and one is that the spoilage pattern described occurs only in a predominantly aerobic environment, such as exists in fish entirely surrounded by ice. The bacteria at this stage of spoilage are chiefly confined to the surface areas of the fish and are therefore working under aerobic conditions. Any sulphydryl compounds formed would probably be oxidized as fast as they are produced either by bacteria or by direct atmospheric oxidation. This is not so for bilgy fish. The specific condition under which bilgy fish are encountered is when the slimy fish have been pressed tightly against wet, soggy

wooden pen boards. Here, the exclusion of the air, together with the very large numbers of bacteria that are present on the surfaces of the fish and boards, soon bring about an anaerobic environment. Under these conditions one would expect that sulphur would be reduced almost completely to hydrogen sulphide. The results with the bilgy fish show that hydrogen sulphide is formed in considerable amounts. It is also shown that mercaptans are formed in the aerobic decomposition, whereas hydrogen sulphide is produced in anaerobic decomposition.

It is not suggested that the characteristic vile odour of bilgy fish is caused solely by hydrogen sulphide. There are undoubtedly other obnoxious compounds present, frequently including relatively large concentrations of TMA and volatile acids. The results do indicate, however, that hydrogen sulphide is present in bilgy fish in amounts sufficient to enable this compound to be used as a measure of this particular type of spoilage.

SUMMARY

(1) Hydrogen sulphide does not accumulate in the muscle of well-iced, dressed cod or haddock until it has reached the very offensive putrid stage.

(2) Hydrogen sulphide does accumulate in the muscle of fish developing bilgy odours. This occurs only in an anaerobic environment and is accompanied by an increase in the anaerobic bacteria.

(3) In these experiments the bilgy odour became evident in the muscle of fish jammed up against heavily contaminated wood surfaces only when the hydrogen sulphide content reached approximately 0.05 mg. per 100 g. of fish.

(4) A limited number of tests indicates that mercaptans develop in the muscle of "normally spoiling", well-iced fish during the earlier stages of spoilage where no hydrogen sulphide has accumulated. In contrast to this, as hydrogen sulphide forms in bilgy fish, the mercaptan content decreases.

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Processing of Cod and Haddock Viscera: 1. Laboratory Experiments[1]

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ABSTRACT

Annually, large amounts of cod and haddock viscera (minus livers) are discarded by the fishing industry. The chemical composition of this offal makes it a possible raw material for production of additives to animal feeds. Various processes that would lead to a method of production of such preparations were investigated. Autolysis of fresh viscera in the presence of sodium nitrite as a preservative was found most attractive. Optimum conditions for this process were established and various methods of drying these autolysates were investigated.

INTRODUCTION

Commercial cod and haddock fishing, at the present time, is a rather wasteful operation: about one-sixth of each fish caught is removed and thrown away. This waste material consists of guts and stomachs and will be referred to as the "viscera" (i.e., total viscera less livers). The amounts wasted annually are very large. No accurate figures are known, but for Nova Scotia alone, a fair estimate of the annual waste is 40,000,000 pounds and for the combined cod and haddock fishery of the Atlantic coast of Canada about 135,000,000 pounds[2]. The approximate gross composition of this raw visceral material was found to be: moisture, 80%; protein (N $\times$ 6.25), 10 to 12%; fat, 1 to 2%; ash, 2 to 3%; and besides these gross constituents, it contains B-vitamins and possibly a number of unidentified growth factors.

Clearly, it would be advantageous to the industry if the waste material could be converted into a by-product of sufficient commercial value. Several possibilities exist in this respect; the most promising seems to be the production of an animal feed. If the viscera could be converted, by a simple process, into a product which could be added to rations for farm animals, a market for such a product would be readily available, particularly if its nutritional quality were especially high or of an especially interesting nature.

During the past 2 years, experiments have been carried out to establish a suitable method for processing of cod and haddock viscera. The procedure finally adopted involves autolysis of the raw material in the presence of sodium nitrite at a slightly elevated temperature and drying of the autolysate. This process was applied to several batches of viscera on a laboratory scale, as well as on a pilot plant scale.

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[2]These figures are based on a yield of 20% viscera from the 1955 landings of cod and haddock (heads on, guts out), the latter reported by the Dominion Bureau of Statistics (1955).

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The present paper will describe the experimental work, done in the laboratory, which led to the final process; a second paper will follow with details regarding pilot plant studies and cost calculations.

EXPERIMENTAL

Materials

Cod and haddock viscera. Stomachs and intestinal tracts obtained from cod and haddock within 24 hours after the fish were caught; livers were removed as completely as possible.

Enzymes. Pepsin: Nutritional Biochemicals Corporation, Cleveland, Ohio. Papain: British Drug Houses, Toronto, Ont. Rhozyme P-11: Rohm and Haas Company, Philadelphia, Pa. Takamine Protease and H.T. Proteolytic: Takamine Laboratory, Incorporated, Clifton, N.J.

Vitamins and amino acids. Nutritional Biochemicals Corporation, Cleveland, Ohio.

Microbiological assay media. Difco Laboratories, Incorporated, Detroit, Mich.

Other chemicals and reagents. Chemically pure or better.

Methods of Analysis

Moisture and solids. Samples are dried overnight at 100 to 105°C.

Soluble solids. Solids determined on the clear solutions obtained after centrifugation and filtration of digests.

Total nitrogen. Micro-Kjeldahl (catalyst: copper sulphate, selenium, sodium sulphate).

Chromogenic nitrogen. Spies and Chambers (1951).

Total chromogenic nitrogen. Chromogenic nitrogen determined on samples, completely hydrolysed with hydrochloric acid.

Fat. Exhaustive extraction (Soxhlet) with light petroleum (30 to 60°).

Ash. Association of Official Agricultural Chemists (1955).

Nitrite. Dyer (1946).

Thiamine. Thiochrome method, after purification with Decalso, according to the Association of Vitamin Chemists (1951).

Riboflavin, niacin, pantothenic acid. Microbiological assay according to the Association of Vitamin Chemists (1951), using Difco's assay media.

Vitamin B_{12}. Microbiological assay as described by Truscott, Gage and Hoogland (1954).

Cholesterol. Foldes and Wilson (1950).

Results

DIGESTION WITH VARIOUS ENZYMES

To 250-g. samples of fresh viscera were added 200 g. of water and certain amounts of various proteolytic enzyme preparations. The mixtures, after adjustment of the pH with acid or alkali, were held at certain temperatures for 2 weeks. At regular intervals samples were withdrawn from each mixture; these were

filtered and washed, and the solid contents of the filtrates were determined. The amount of soluble solids (SS), expressed as the percentage of the total solid content (TS) of the original sample, was used to indicate the extent to which digestion had progressed. Occasionally, these values were expressed as the ratio of soluble chromogenic nitrogen (CN) to total chromogenic nitrogen (TCN). The latter results agreed reasonably with the SS/TS ratios for the same samples; the advantage was the rapidity with which they could be determined.

The relationship between the extent of the digestion and the time of digestion showed a pattern which was very similar for all treatments. Some typical curves in Fig. 1 show that the digestion proceeded to a maximum which was reached under certain conditions of pH and temperature after a certain length of time. This maximum value was determined for each treatment. The values found and the times required to reach those values are listed in Table I.

It was concluded from these results that addition of enzymes to the viscera offered no advantages; apparently, sufficient amounts of enzymes were available in the raw material. The rate of digestion and the maximum effect were practically the same for all treatments.

It was decided to investigate further simple autolysis as a means of digesting viscera.

TABLE I.—Digestion of viscera with and without added enzymes at different temperatures and pH.

Test No.	Enzyme added	Amount added	Temp.	pH	Digestion maximum[b] SS/TS	Digestion maximum[b] CN/TCN	Time required to reach maximum
		%[a]	°C.		%	%	*days*
1	None	...	25	3.5	84.5	...	4
2	"	...	25	4.0	89.0	...	4
3	"	...	25	4.5	80.0	...	3
4	"	...	37	1.0	82.4	...	3
5	"	...	37	2.0	85.5	...	3
6	"	...	37	3.0	87.8	...	3
7	"	...	37	4.0	87.5	84.9	3
8	"	...	37	5.5	86.1	85.7	3
9	"	...	37	6.8	93.6	86.0	3
10	"	...	37	7.2	91.8	...	3
11	"	...	37	8.0	86.1	87.0	3
12	"	...	50	2.0	90.0	...	2
13	Pepsin	1	37	1.0	89.0	...	3
14	"	1	37	2.0	85.1	...	3
15	"	1	37	4.0	87.2	84.2	3
16	Papain	1	37	4.0	87.2	84.9	3
17	Rhozyme P-11	1	37	4.0	...	82.9	3
18	Takamine protease	1	37	4.0	...	83.4	3
19	"	1	37	8.0	90.2	...	3
20	"	1	50	8.0	90.3	...	3
21	H.T. proteolytic	1	37	8.0	89.0	...	2

[a]Based on moisture-free raw material.
[b]For significance of abbreviations, see text.

AUTOLYSIS AT VARIOUS TEMPERATURES AND ACIDITIES

A batch of viscera was frozen and then minced with a meat grinder. After thawing, 250-g. samples were subjected to autolysis under various conditions. Digestion curves were determined for each treatment. The results are given in Fig. 1.

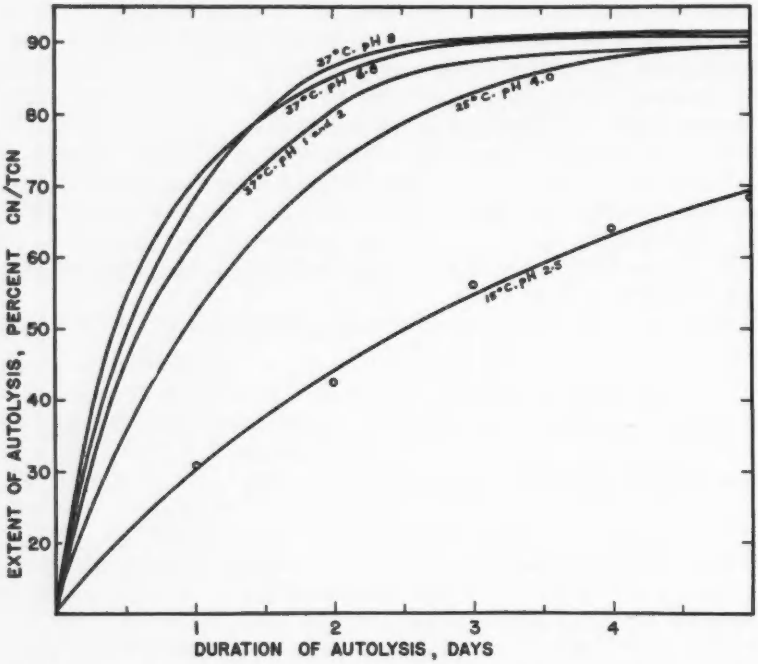

FIG. 1.—Progress of autolysis of cod viscera at various temperatures and pH. (To avoid confusion, the points used for plotting of the curves are given for one curve only; CN/TCN=soluble/total chromogenic nitrogen.)

The effect of temperature on the rate of autolysis was as expected. At 37°C., autolysis progressed rapidly; at 25°C., slightly more slowly, and at 15°C. it had become very slow. In practice, autolysis at 37°C. or at 25°C. could be used; the selection of a temperature would probably depend on the processing cost and the availability of equipment. Further laboratory experiments were carried out at 37°C.

A choice of pH could not be made as easily. There appeared to be little, if any, effect of pH in the range of 1 to 8 on the rate of autolysis; the maximum was about the same for all treatments. Obviously, it would be most convenient to carry out the autolysis at the natural pH of the viscera; no labour would be required for pH adjustment and the autolysate would be practically neutral, a

desirable property for material that will be used in animal feeds. However, this introduced the problem of spoilage: when autolysis was carried out at pH 6.5 to 7.5, samples of viscera rapidly produced very offensive spoilage odours. At pH 3 or in more acid surroundings, this spoilage did not occur, but such autolysates required neutralization before drying and hence the dried products contained large amounts of salt. To avoid this, two preservatives were investigated for their ability to inhibit spoilage sufficiently and permit autolysis at the natural pH of the viscera or at a pH only slightly lower, when added to the fresh raw material.

PREVENTION OF SPOILAGE OF THE VISCERA

Fresh cod and haddock viscera were frozen, then minced with a meat grinder. To 250-g. portions of this mixture, after adjusting the pH if necessary, sodium nitrite or methyl parasept (methyl parahydroxybenzoate) was added and the samples were incubated at 37°C. for 2 weeks. They were inspected daily for spoilage (objectionable odours).

Methyl parasept, in concentrations up to 1 g. per 500 g. of raw material, did not postpone spoilage for longer than a few days. Higher concentrations of the preservative did lengthen the keeping time but they were considered impracticable from the viewpoint of cost and also because the dried end-product would contain too large an amount of methyl parasept.

Very encouraging results were obtained with sodium nitrite. Table II lists the keeping times of samples after addition of sodium nitrite in different concentrations at pH 6.8, the natural pH of the raw material, and at pH 5.5.

Sodium nitrite was more effective in prolonging the keeping time at pH 5.5 than at pH 6.8; however, at both acidities, at least 1000 μg./g. (0.1%) was needed to extend the keeping time of the raw material to 2 weeks, which was considered the necessary minimum period required for practical application.

This amount seemed rather high and would certainly not be permissible, if during autolysis and subsequent drying no nitrite were lost. It was demonstrated,

TABLE II.—Effect of sodium nitrite on the keeping time of viscera at 37°C. and pH 5.5 and 6.8.

Concentration of sodium nitrite	pH	Sample acceptable for:	Sample spoiled after:
μg./g.		*days*	*days*
0	5.5	1	2
100	5.5	7	14
150	5.5	7	14
200	5.5	7	14
250	5.5	10	14
1000	5.5	>14	...
0	6.8	½	1
100	6.8	3	5
200	6.8	3	5
500	6.8	4	5
1000	6.8	>14	...
1500	6.8	>14	...
2500	6.8	>14	...

however, that the nitrite concentration diminished steadily during autolysis. This is shown in Fig. 2 for an autolysate of which the nitrite concentration dropped from 1000 μg./g. to about 400 μg./g. in 3 days. It will be shown below that this value was low enough to ensure that after drying, during which still more nitrite was destroyed, not more than 200 μg./g. would remain.

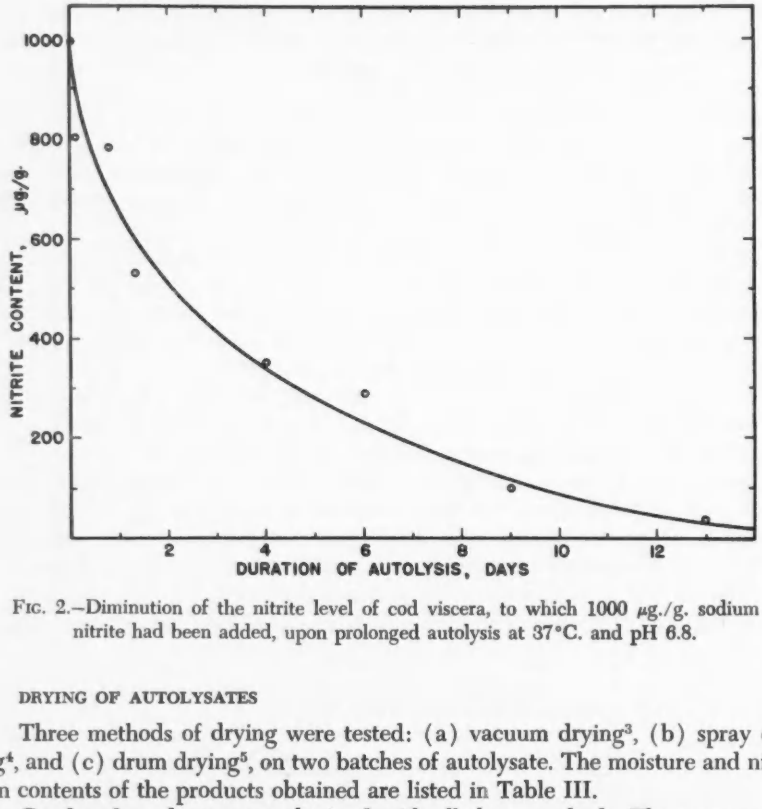

FIG. 2.—Diminution of the nitrite level of cod viscera, to which 1000 μg./g. sodium nitrite had been added, upon prolonged autolysis at 37°C. and pH 6.8.

DRYING OF AUTOLYSATES

Three methods of drying were tested: (a) vacuum drying[3], (b) spray drying[4], and (c) drum drying[5], on two batches of autolysate. The moisture and nitrogen contents of the products obtained are listed in Table III.

Good end-products were obtained with all three methods. The appearances were slightly different: after vacuum drying and grinding, the meal was yellowish brown; spray drying produced a very fine, slightly yellow powder; drum drying followed by grinding gave a somewhat darker coloured powder. Drum drying was chosen as the most useful method because of its much lower cost.

[3]All-glass laboratory still, temperature not above 60°C.

[4]Laboratory spray dryer, Dominion Scott Barrow Ltd., Toronto, Ont., inlet temperature 200°C., outlet temperature 71°C.

[5]Atmospheric double-drum dryer, laboratory model, Buflovak Equipment Division of Blaw-Knox Co., Buffalo, N.Y., steam gauge pressure 1.75 kg./cm.^{2} (25 lb./sq. in.), drum speed 3 r.p.m.

TABLE III.—Moisture and nitrogen contents of dried visceral autolysates.

Batch No.	Drying method	Moisture content	Nitrogen content
		%	%
1	Vacuum	10.1	11.6
	Spray	9.2	11.6
	Drum	8.3	11.5
2	Vacuum	9.1	10.8
	Spray	4.6	10.8
	Drum	4.2	10.9

The effect of drum drying on the nitrite content of autolysates, prepared from viscera to which 0.1% sodium nitrite had been added, was studied. Seven different autolysates were dried; their nitrite contents varied from 200 to 560 μg./g. (on a moisture-containing basis) before drying. After drying, the meals contained 11, 46, 52, 63, 82, 126 and 184 μg./g. respectively. This was considered acceptable for preparations which are to be used as additives to animal feeds. The addition of 0.1% sodium nitrite to the raw material was hence sufficient to prevent spoilage and low enough to avoid occurrence of excessive amounts of nitrite in the finished meal.

CHEMICAL COMPOSITION OF DRIED AUTOLYSATES

Fifteen pounds of fresh cod and haddock viscera, to which 0.1% sodium nitrite had been added, was autolysed for 4 days at 37°C. and pH 6.9 (the natural pH). Following autolysis, the solution was centrifuged and then divided into three portions, which were dried by the three methods given above. The meals obtained in this manner were analysed for moisture, nitrogen, fat, ash, nitrite and several B-vitamins. The results are listed in Table IV.

The compositions of the meals were very similar; the only significant differences occurred in the nitrite contents. Much more nitrite had been destroyed during the drum drying and vacuum drying procedures than during spray drying. All three meals were yellowish brown, and slightly hygroscopic. They were readily dispersible in water; 77% of the solids was water-soluble.

TABLE IV.—Chemical composition of three visceral meals obtained from one batch of autolysate by vacuum drying, spray drying, and drum drying.

Constituent	Vacuum dried	Spray dried	Drum dried
Moisture, %	7.9	8.6	7.4
Total nitrogen, %	11.70	11.54	11.47
Fat, %	...	4.48	5.94
Ash, %	8.87	8.94	8.92
Nitrite, μg./g.	11.9	43.4	17.1
Thiamine, μg./g.	1.26	1.05	1.30
Riboflavin, μg./g.	14.4	16.8	14.4
Niacin, μg./g.	69	69	66
Pantothenic acid, μg./g.	51	82	79
Vitamin B_{12}, μg./g.	0.88	0.88	0.76

DISCUSSION

The reason why such a readily available waste material as the viscera of cod and haddock has not been generally used in a by-products industry is that no convenient method of handling and processing had been developed. The problems of preserving the viscera and of pumping the material from tanks aboard ship to containers ashore have discouraged such usage. The processing method described above is considered to have overcome these problems, and industrial application of the method is visualized.

Direct drum drying of autolysates produced very satisfactory meals which after grinding may be packed in any kind of a moisture-proof container (paper bags with plastic lining have proved very useful). However, a number of other possible processing methods are now under investigation in this laboratory:

1. The autolysate may be evaporated to form a liquid concentrate with standardized solid content.

2. The autolysate may be passed through a filter press to clarify it and the clear liquid then concentrated or dried. After this treatment, the end-product will be completely water-soluble.

3. Evaporation and drum drying of the autolysate may be combined to provide a more economical production process.

4. Either the liquid preparations or the meals may be defatted by solvent extraction. The oil obtained in this manner was found to contain a high proportion of cholesterol (9 to 12%) which may be isolated and prepared in a pure form by standard procedures. The defatted preparations may be further concentrated or dried. Material obtained in this manner proved to be of very good quality and may be used in various food products.

5. Any one of the preparations may be used as the starting material for secondary by-products. Of particular interest are protein digests for the food industry, for bacteriological media, or for the preparation of amino acids. The production of lysine for enrichment of foods is considered an important possibility.

It should be emphasized that the analytical data given for various constituents of a drum-dried autolysate do not necessarily represent the average composition of meal prepared on a large scale. At present, a study of the variability of the chemical composition of visceral meals, prepared from different batches of raw material, is being carried out. The number of samples analysed is still too small to warrant publication of the results. One finding was obvious; the fat content of autolysates is largely dependent on the extent to which livers have been removed from the viscera. With hardly any livers remaining in the raw material, drum-dried meals contained about 5% fat having a cholesterol content of 9 to 12%. When livers were left in, however, the fat content of the meal increased and, consequently, the cholesterol content of the fat decreased.

The study of the chemical composition of autolysates and its variation is nearly completed. Pilot plant experiments regarding the production of a drum-dried meal have been carried out and estimates of production costs are being prepared.

SUMMARY

1. The rate of digestion of cod and haddock viscera at 15°, 25°, and 37°C. was not affected by the addition of proteolytic enzymes.

2. The effect of pH between 1 and 8 on the extent of the digestion was negligible.

3. Addition of 0.1% sodium nitrite to fresh viscera, at the natural pH of the raw material, prevented spoilage at 37°C. for at least 2 weeks, and was adopted as a standard treatment.

4. Autolysis usually reached a maximum after 3 days at 37°C.

5. At this maximum, 80 to 90% of the total solids of the raw material was soluble in water.

6. Such liquid autolysates were dried in a number of ways. For production of a meal, drum-drying proved very practical.

7. The nitrite content of finished meals was lower than 200 μg./g.

8. The chemical composition of the finished meals showed that they are good sources of nitrogen and B-vitamins.

9. Further work, on a pilot plant scale, is in progress to determine production costs, and data regarding the chemical composition, that may be expected if the process is attractive to the industry.

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